Coral reef functioning in a highly variable environment

- Effects of upwelling on Pacific coral reefs of Costa Rica -

A dissertation by

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'The sea, once it casts its spell, holds one in its net of wonder forever.'
Jacques Yves Cousteau

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Abstract

With increasing local and global stressors on coral reef ecosystems, the future stability of environmental conditions for coral reefs is in question. The capacity of reef organisms and ecosystems to adapt to such variable environments in terms of functions and services is a current topic in coral reef research, yet related knowledge, especially on the ecosystem level, is scarce. Marginal reefs that thrive in highly fluctuating or limiting environments, such as upwelling systems, provide natural laboratories to study the acclimatization and adaptation potential of reef organisms. This thesis aimed to contribute to the understanding of coral reef functioning in variable environments by investigating the impact of the Papagayo upwelling at the northern Pacific coast of Costa Rica. A series of interconnected studies was conducted in upwelling exposed reefs at weekly intervals over an entire observation year (April 2013 - April 2014). These studies monitored (i) a range of inorganic and organic water parameters, (ii) in situ primary production rates, (iii) benthic and herbivore community composition, and (iv) responses of algal and invertebrate settlement to simulated overfishing. Upwelling events between February and April 2014 decreased water temperatures by 7 - 9 °C for several hours or days, while inorganic nutrient concentrations increased 3 - 16-fold. Sequentially, organic matter concentrations in the water column above the reef doubled and remained elevated for 2 - 3 months (Chapter 2). Surprisingly, the strong seasonality in environmental conditions did not significantly influence benthic community productivity or composition in the studied reef. Upwelling-impacted water parameters negated each other in their effects on primary production of reef organisms. Corals were the only primary producers that benefitted from upwelling conditions, while production rates of all investigated algal taxa decreased (Chapter 3). Instead of following a seasonal cycle, benthic cover of the scleractinian corals *Pocillopora* spp. increased continuously and at an exceptionally high rate over the monitoring year (from 20 % to 50 % relative cover), while turf algal cover dropped significantly (from 60 % to 20 %). This shift in community composition was supported by high abundances of the herbivorous sea urchin *Diadema mexicanum*, which controlled turf algal cover in the reef community (Chapter 4). Fish exclusion significantly altered benthic communities on settlement tiles from short turf algae and crustose coralline algae dominance towards long turf algae, fleshy macroalgae and ascidians (Chapter 5). The results of this thesis indicate that the investigated benthic reef community is physiologically acclimatized to seasonal changes in environmental con-

ditions, and that the local herbivore community effectively controls algae growth in the studied reef. However, high abundances of sea urchins potentially threaten the reef structure through bioerosion, and overexploitation of herbivorous reef fish may result in benthic community shifts. Additionally, repeated disturbances such as coral diseases (Chapter 6), El Niño events and harmful algal blooms likely prevent the coral community from increasing in diversity or developing a resistant reef structure. Upwelling-influenced reefs in the Gulf of Papagayo provide an example of how reefs may look like in the future, when anthropogenic chronic stressors will select for a minority of resilient coral species to dominate reef ecosystems. The results of this thesis suggest that those future reefs may still be highly productive and have a high resilience towards prevailing stressors in their ecosystem. Despite this, the reefs will be vulnerable to the intervention of acute stressors such as disease outbreaks or El Niño events due to low genetic diversity and functional redundancy in the coral populations.

Zusammenfassung

Zunehmende lokale und globale Stressfaktoren auf Korallenriffökosysteme bedrohen die Stabilität der Umweltbedingungen in den Korallenriffen der Zukunft. Die Fähigkeit von Rifforganismen und -ökosystemen ihre Funktionen und Leistungen an solche variablen Umgebungen anzupassen ist ein aktuelles Thema in der Korallenriffforschung, aber bisherige Kenntnisse, insbesondere auf dem Ökosystemlevel, sind begrenzt. Marginale Riffe die in sehr variablen oder limitierenden Umgebungen vorkommen, zum Beispiel in Auftriebsgebieten, stellen natürliche Labore dar, in denen das Akklimatisations- und Anpassungspotenzial von Rifforganismen studiert werden kann. Das Ziel dieser Dissertation war es, zum Verständnis der Funktionsweise von Korallenriffen in variablen Lebensräumen beizutragen. Dafür wurde exemplarisch der Einfluss des Papagayo Auftriebs an der nördlichen Pazifikküste von Costa Rica untersucht. Über ein komplettes Jahr (April 2013 - April 2014) wurde in Auftriebs-exponierten Korallenriffen eine Reihe von vernetzten Studien in wöchentlicher Auflösung durchgeführt. Diese Studien beobachteten (i) eine Vielzahl an anorganischen und organischen Wasserparametern, (ii) in situ Primärproduktionsraten, (iii) benthische und herbivore Gemeinschaftsstrukturen und (iv) die Effekte von simulierter Überfischung auf Algen und Wirbellose. Auftriebsereignisse in der Zeit von Februar bis April 2014 reduzierten die Wassertemperatur um 7 - 9 °C für mehrere Stunden oder Tage, während Nährstoffkonzentrationen um das 3 - 16-fache anstiegen. Konzentrationen an organischem Material in der Wassersäule verdoppelten sich daraufhin und blieben für 2 - 3 Monate erhöht (Kapitel 2). Überraschenderweise hatte die ausgeprägte Saisonalität in den Umweltbedingungen keinen signifikanten Einfluss auf die Produktivität oder Struktur der untersuchten benthischen Riffgemeinschaft. Die vom Auftrieb beeinflussten Wasserparameter negierten sich gegenseitig in ihrem Effekt auf die Primärproduktion von Rifforganismen. Korallen waren die einzigen Primärproduzenten die vom Auftrieb profitierten, während sich die Produktionsraten aller untersuchter Algengruppen verringerten (Kapitel 3). Anstatt einem saisonalen Verlauf zu folgen stieg der relative Bewuchs durch die Steinkoralle *Pocillopora* spp. über das Beobachtungsjahr kontinuierlich und in außerordentlicher Geschwindigkeit an (von 20 % auf 50 %), während die Bedeckung durch filamentöse Algen sank (von 60 % auf 20 %). Diese Verschiebung in der benthischen Gemeinschaftsstruktur wurde begünstigt durch eine hohe Abundanz an herbivoren Seeigeln (*Diadema mexicanum*), welche die filamentösen Algen im Riff kontrollierten (Kapitel 4). Simulierte Überfischung resultierte in deutli-

chen Veränderungen der benthischen Gemeinschaften auf Besiedlungsplatten von kurzen filamentösen Algen und Krustenalgen hin zu langen filamentösen Algen, Makroalgen und Seescheiden (Kapitel 5). Die Ergebnisse dieser Arbeit deuten darauf hin, dass die untersuchte Riffgemeinschaft an saisonale Veränderungen der Umweltbedingungen akklimatisiert ist, und dass die lokale Gemeinschaft an Herbivoren effektiv das Algenwachstum im Riff kontrolliert. Allerdings gefährdet die hohe Anzahl an Seeigeln durch Bioerosion möglicherweise die Stabilität der Riffstruktur, und Überfischung von herbivoren Fischen könnte zu Veränderungen in den benthischen Gemeinschaftsstrukturen führen. Darüberhinaus verhindern wiederholte Störungen, wie zum Beispiel Korallenkrankheiten (Kapitel 6), El Niño Ereignisse und giftige Algenblüten, wahrscheinlich eine Zunahme der Biodiversität und den Aufbau einer beständigen Riffstruktur. Die Korallenriffe im Golf von Papagayo sind ein Beispiel dafür, wie Riffe in der Zukunft aussehen könnten, wenn menschengemachter chronischer Stress zur Selektion und Dominanz weniger Korallenarten führt. Die Ergebnisse dieser Arbeit legen nahe, dass jene Riffe immer noch sehr produktiv sein könnten und gut an die vorherrschenden Stressoren in ihrem Ökosystem angepasst sind. Sie werden sich wegen der geringen genetischen Diversität und der geringen funktionellen Redundanz innerhalb der Korallenpopulationen jedoch nur schlecht vom Einfluss akuter Stressoren wie zum Beispiel Krankheiten oder El Niño Ereignissen erholen.

Contents

1 General introduction

1.1 Coral reef ecosystems: Services versus threats

Coral reef ecosystems are among the most biodiverse and productive ecosystems on earth (Hatcher 1988, Reaka-Kudla 1997). As ecosystem engineers, scleractinian corals secrete a calcium carbonate skeleton which builds the framework of a coral reef (Gutiérrez et al. 2011, Wild et al. 2011). Other calcifying organisms such as coralline algae and invertebrate species further contribute to the cementation and structural complexity of this framework (Fagerstrom 1987, Chisholm 2000). The ecosystem's high complexity provides habitat and protection, supports important functions such as spawning, and provides a nursery, breeding and feeding ground to a magnitude of organisms (Moberg & Folke 1999). While covering less than 0.1 % of the world's ocean surface (Spalding et al. 2001), coral reefs shelter approximately 34 % of currently described marine species, including fish, crabs, mollusks, sponges and algae (Reaka-Kudla 1997), and thereby provide a precious biological diversity and genetic library for future generations (Moberg & Folke 1999). Despite generally thriving in nutrient-poor waters, coral reefs support levels of productivity several orders of magnitude higher than that of surrounding areas (Odum & Odum 1955, Hatcher 1988). This high productivity is supported by the symbiosis between scleractinian corals, photosynthesizing symbiotic algae of the genus *Symbiodinium*, and a consortium of associated bacteria, fungi and archaea (Rohwer et al. 2002, Rosenberg et al. 2007). Nutrients are efficiently recycled within the coral holobiont (Wegley et al. 2007) and within the entire reef ecosystem (Muscatine & Porter 1977, Wild et al. 2011) which partly explains the 'Darwin's Paradox' of sustaining high productivity in a nutrient poor environment. High productivity is a key ecosystem service of coral reefs and not only beneficial for marine organisms. To humans, reef ecosystems provide coastal protection from hurricanes and erosion, food and livelihoods for coastal communities, income from tourism, provision of substances for pharmaceutical purposes, and of course aesthetic value (Moberg & Folke 1999, Sale 2008). Approximately 500 million people are directly dependent on coral reefs (Wilkinson 2008), and the net benefits of coral reefs worldwide per year are estimated to account for US$ 30 - 375 billion (Costanza et al. 1997, Cesar et al. 2003).

The ability of coral reefs to persist in the future is threatened by human pressures and climate change. Predictions suggest that 60 % of all coral reefs could be lost by the year

2030 (Hughes et al. 2003, Wilkinson 2008). Local human stressors include fishing pressure, nutrient enrichment, sedimentation and pollution (Hughes 1994, Jackson et al. 2001, Pandolfi et al. 2003). These stressors can push a healthy coral reef, dominated by corals and crustose coralline algae, to a degraded ecosystem, dominated by alternative organisms including turf algae, cyanobacteria, fleshy macroalgae or invertebrates other than hard corals (Done 1992, Norström et al. 2009). The relative importance and interactions of stressors in driving these phase-shifts vary geographically and locally, which complicates effective management for reef conservation.

Besides local pressures, coral reefs face an increasing threat from global stressors linked to climate change. Ocean warming and acidification, caused by the continuous and increasing emission of greenhouse gases, lead to widespread and long-lasting changes in the physicochemical environment of the World's oceans (Howes et al. 2015). Warming of the ocean's surface increases stratification of the water column, thereby limiting the circulation of nutrients and oxygen between water layers (Rhein et al. 2013). Further, it pushes sensitive marine organisms, including scleractinian corals, to their physiological limits (Hoegh-Guldberg et al. 2007). By decreasing the carbonate saturation state of the water, ocean acidification decreases calcification in scleractinian corals and thereby reduces net coral reef community calcification (Cohen & Holcomb 2009, Comeau et al. 2014). Reefs which have been degraded as a combined result of climate change effects and local disturbances are no longer able to provide the ecological services of a healthy coral reef (Wild et al. 2011).

The potential of coral reefs to adapt to future environmental changes is still under debate (Berkelmans & van Oppen 2006, Hoegh-Guldberg 2011) and will depend on the ability of species to adapt to unprecedented fast and pronounced changes within their ecosystems.

1.2 Marginal reef ecosystems: Windows in the future

The majority of tropical coral reefs exist in fairly uniform physicochemical environments in tropical and subtropical waters, with their global distribution mainly depending on abiotic factors such as water temperature, light availability, aragonite saturation and nutrients (Kleypas et al. 1999, Couce et al. 2012). However, recent studies have shown that coral reefs can in fact occupy a wide range of environments, characterized by varying sea surface temperatures, nutrient levels, and other physicochemical parameters (Chollett et al. 2012, Freeman et al. 2012, Wang et al. 2015). Some of these environments experience conditions near the tolerance limits of coral reefs, known as "marginal habitats" (Kleypas et al. 1999). Marginality can be defined on the basis of environmental condition which may limit the occurrence of reefs, but also in terms of organism and community condition (low biodiversity, poor reef development, low productivity) (Guinotte et al. 2003). These conditions often, but not always, interact. Suboptimal environments are characterized by high or low

temperatures, salinities, or nutrient levels, or by low light penetration or aragonite saturation states (Perry & Larcombe 2003). Due to local stressors and climate change, many reefs are in danger of becoming marginal in the near future (Guinotte et al. 2003). Coral reefs existing in challenging conditions already today therefore become increasingly interesting for research. These 'natural laboratories' (Fig. 1.1) include under water CO_2 seeps with low water pH and aragonite saturation states (Fabricius et al. 2011, Uthicke & Fabricius 2012), high-latitude reefs with extreme temperatures and pronounced seasonality in conditions (Schleyer & Celliers 2003, Gischler et al. 2005, Goodkin et al. 2011, Riegl & Purkis 2012, Yamano et al. 2012, Fellegara et al. 2013), and upwelling areas with highly variable conditions in space and time (Glynn 1977, Diaz-Pulido & Garzón-Ferreira 2002, Benzoni et al. 2003, D'Croz & O'Dea 2007).

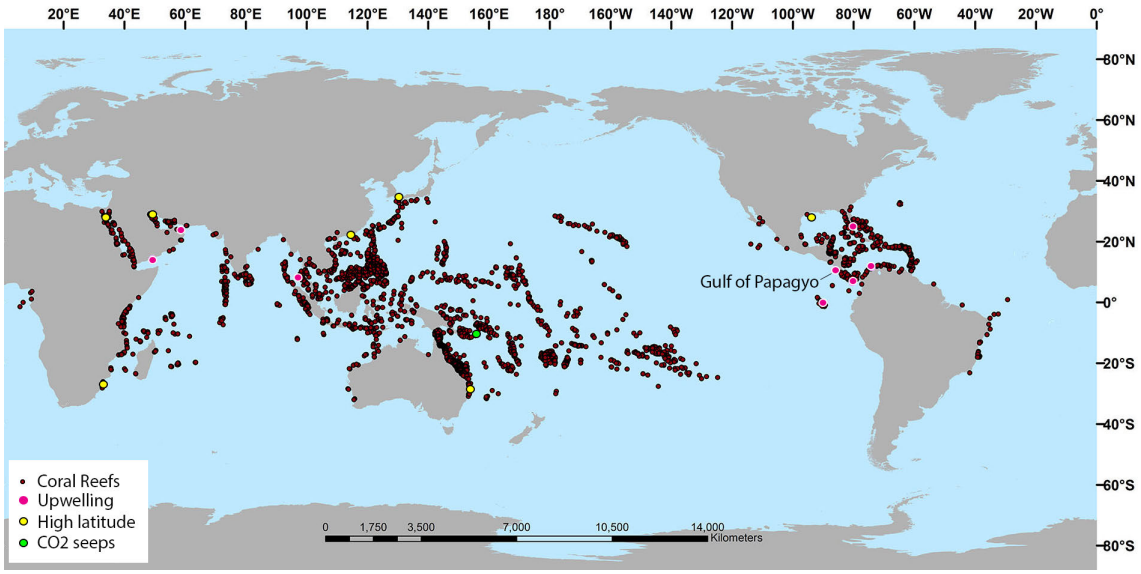

Figure 1.1: Distribution of marginal reefs. Locations of coral reefs worldwide are indicated by dark dots (map adapted from NOAA). Pink, yellow and green dots indicate the locations of marginal reefs that have been used as natural laboratories (studies mentioned in the text). The map also includes the site of the present study, Gulf of Papagayo, at the Pacific coast of Costa Rica.

In upwelling systems, the temporal mixing of surface water with sub-thermocline water causes large variations in the water chemistry on coral reefs: water temperature and pH decrease, while concentrations of inorganic nutrients and dissolved inorganic carbon (DIC) increase (Pennington et al. 2006, Fassbender et al. 2011, Rixen et al. 2012). Comparable changes in conditions are caused by large amplitude internal waves (LAIW) (Schmidt et al. 2012) or high frequency internal bores (Leichter et al. 1996, 2003) which cause temperature anomalies in the scales of minutes to hours. Low- and high-frequency variations in environmental parameters can drive distinct patterns in coral reef benthic community composition and productivity (Leichter et al. 2003, Gove et al. 2015). On a spatial scale, previous

studies found reduced coral growth and reef development at sites exposed to upwelling (Glynn & Stewart 1973, Glynn 1977) and LAIW (Schmidt et al. 2012) compared to protected sites. Contrarily, upwelling can have positive effects on coral health by increasing nutrition and symbiont density in exposed corals (Roder et al. 2010, 2011) and can decrease coral susceptibility to bleaching (Bayraktarov et al. 2012, Wall et al. 2015). On a temporal scale, upwelling can increase relative cover (Diaz-Pulido & Garzón-Ferreira 2002, Fernández-García et al. 2012, Cortés et al. 2014) and primary production of benthic macroalgae on coral reefs (Eidens et al. 2012, 2014). However, studies on temporal impacts of upwelling on the composition and production of entire reef communities are scarce, and the temporal resolution of existing studies is very low.

As global and local stressors will lead to a higher instability of conditions in future coral reefs (Pandolfi et al. 2011), upwelling areas provide important natural laboratories to study the acclimatization (physiological adjustments) and adaptation (genetic modification over generations) potential of coral reefs to instabilities in environmental conditions. To tackle the existing knowledge gaps, observations at a high temporal scale and over an adequate time span are needed.

1.3 Eastern Tropical Pacific: Natural laboratory for highly variable environments

Reefs in the eastern tropical Pacific are marginal regarding both definitions of Guinotte et al. (2003): Marginal due to environmental conditions that push reef organisms to their physiological limit, and marginal according to their ecosystem state, meaning the reefs have low species diversity, poor reef development and are geographically isolated. The Eastern Pacific warm pool is characterized by high sea surface temperatures, coinciding with low salinities and a low aragonite saturation state (Fiedler & Talley 2006, Manzello et al. 2008). These conditions are disrupted in the Gulfs of Tehuantepec (Mexico), Papagayo (Costa Rica - Nicaragua), and Panama (Panamá), where seasonal coastal upwelling causes highly variable conditions in space and time. While the Gulf of Panama has been investigated relatively well regarding upwelling conditions and its influence on local coral reefs (Glynn & Stewart 1973, Glynn 1977, D'Croz et al. 1991, D'Croz & O'Dea 2007), the Gulf of Papagayo remains poorly studied in this respect.

A topographic depression in the lowlands of southern Nicaragua and northern Costa Rica allows strong winds to blow across from the Gulf of Mexico and the Caribbean during the northern hemisphere winter (McCreary et al. 1989, Amador et al. 2006). On the Pacific side, in the Gulf of Papagayo, these wind jets displace superficial water away from the coast, thus causing the shallow thermocline to break the surface (Fiedler & Talley 2006). The seasonal

upwelling decreases mean seawater temperatures from around 28 °C between May and November, down to 23 °C between December and April (Jiménez 2001, Alfaro et al. 2012). During strong upwelling events, water temperature may drop by 8 - 9 °C within hours (Alfaro & Cortés 2012), which is accompanied by decreases in pH and oxygen concentration (Rixen et al. 2012) and peaks in nutrient concentrations (Fernández-García et al. 2012). While remote sensing and open water sampling already described some physical aspects of the Papagayo upwelling, the spatial and temporal effects on key parameters and processes in reef waters have not yet been investigated, although being highly relevant for coral reef functioning. Previous studies mention the potential limiting effects of seasonal upwelling on coral reefs in the Gulf of Papagayo (Glynn et al. 1983, Cortés 1997), but its impacts on temporal dynamics in benthic community composition and functioning are not known. Reefs in this area are relatively small and composed of few reef-building coral species, but sustain a high diversity of associated organisms, thereby providing 'minimum examples of coral reefs' (Cortés 1997). The predictable seasonal changes in water parameters and the occurrence of relatively simple, easily accessible coral reef communities make the Gulf of Papagayo an ideal natural marine laboratory for studying the effects of highly variable environmental conditions on coral community structure and functioning.

1.4 Knowledge gaps and objectives of this thesis

Global and local stressors are projected to lead to higher instability of conditions in future coral reefs. We still do not understand if and how coral reefs and reef organisms will adapt to these environmental changes. Studies in aquaria and mesocosms are manifold, but are limited in their implications for ecosystem responses. It is therefore critically important to conduct in situ studies investigating the effects of changing conditions on coral reef functioning. Ecosystem studies in highly variable environments are scarce, because they are time-consuming, poorly predictable and restricted to specific and spatially limited areas such as upwelling regions. Previous studies in upwelling areas mainly focused on spatial differences in benthic communities comparing exposed versus sheltered sites, while studies on temporal variability in benthic community composition and production in response to upwelling are practically nonexistent.

This thesis aims to contribute to the understanding of coral reef communities in extremely variable environments and how they may perform under future conditions. The main goal was to understand the impact of the Papagayo upwelling on local coral reef benthic community composition and functioning. Despite ongoing research in this area for three decades, this topic has received very little attention. The overall research questions of this thesis were:

1. **How does the upwelling affect water column parameters relevant for coral reef functioning on both spatial and temporal scales?**
2. **How does the variability in environmental conditions affect coral reef benthic community composition and functioning?**
3. **What is the ecological perspective for local reefs now and in the future?**

1.5 Approach and thesis outline

This study was conducted in collaboration with the Centro de Investigación en Ciencias del Mar y Limnología, San Jose, Costa Rica. The collaboration was initiated by C. Wild, T. Rixen, J. Cortés and A. Morales in 2012.

The primary work was carried out in the province Guanacaste at the northern Pacific coast of Costa Rica from March 2013 until May 2014. All conducted monitoring and experimental work took place in situ at upwelling-influenced coral reefs which served as natural laboratories for highly variable environments.

Publication outline

This thesis includes five manuscripts, whereof two have already been published (Chapters 5 & 6), while three others are under revision or in review at international peer-reviewed journals (Chapters 2, 3, 4). Together, these studies provide a holistic view of how coral reefs in the eastern tropical Pacific respond to upwelling conditions. The manuscripts are embedded in a general thesis introduction (Chapter 1) and a general discussion of all thesis findings and wider implications for coral reefs (Chapter 7).

In the first study (Chapter 2), we monitored the temporal variability in a range of water parameters essential for coral reef functioning. Monitoring was conducted on two coral reefs differently exposed to upwelling in a weekly to monthly temporal resolution over a period of one year. The goal was to describe how long, and to what extent, key water column parameters are influenced by seasonal wind-driven upwelling. In the second study (Chapter 3), we quantified individual primary production rates of the dominant primary producers, and total net and gross primary production of an upwelling-exposed reef in a weekly to monthly resolution over one year. The influence of seasonally changing environmental parameters on net primary production rates was analyzed for each investigated organism group. In the third study (Chapter 4), we analyzed the temporal variability in benthic community composition of an upwelling exposed reef in a weekly resolution over one year of monitoring. Changes in benthic community composition were related to herbivore abundances and key water parameters in order to identify the driving factors of local reef

functioning, and to develop an ecological perspective for local coral reefs. In the fourth study (Chapter 5), we used fish exclusion cages and settlement tiles to assess the impact of overfishing on the succession of benthic algae and invertebrate communities. Simultaneously, we determined the effects of seasonal nutrient input via upwelling on settler communities and initial algal recruitment. The last manuscript of this thesis (Chapter 6) reports large-scale coral mortality at the investigated reef in 2012, which is relevant for the evaluation of ecological perspectives for local reefs, reflected upon in the general discussion.

Publication 1

Ines Stuhldreier, Celeste Sánchez-Noguera, Tim Rixen, Jorge Cortés, Alvaro Morales, Christian Wild

Seasonal upwelling controls organic matter cycles above eastern tropical Pacific coral reefs

The study was designed by I. Stuhldreier and C. Wild. The data acquisition was conducted by I. Stuhldreier and C. Sánchez-Noguera. The data was analyzed by I. Stuhldreier and the manuscript was written by I. Stuhldreier with support of all authors. This article is under revision at PLOS ONE.

Publication 2

Ines Stuhldreier, Celeste Sánchez-Noguera, Florian Roth, Jorge Cortés, Tim Rixen, Christian Wild

Seasonal changes in coral reef primary production at the upwelling-influenced Costa Rican Pacific coast

The study was designed by I. Stuhldreier and C. Wild. The data acquisition was conducted by I. Stuhldreier, C. Sánchez-Noguera and F. Roth. The data was analyzed by I. Stuhldreier and the manuscript was written by I. Stuhldreier with support of all authors. This article is in review at Frontiers in Marine Science.

Publication 3

Ines Stuhldreier, Celeste Sánchez-Noguera, Florian Roth, Carlos Jiménez, Tim Rixen, Jorge Cortés, Christian Wild

Benthic community shift in an upwelling-exposed coral reef on the Pacific coast of Costa Rica

The study was designed by I. Stuhldreier and C. Wild. The data acquisition was conducted by I. Stuhldreier, C. Sánchez-Noguera and F. Roth. C. Jiménez provided further observations and expertise for the discussion of findings in a broader context. The data was analyzed by I. Stuhldreier and the manuscript was written by I. Stuhldreier with support of all authors. This article is in review at PeerJ.

Publication 4

Florian Roth, Ines Stuhldreier, Celeste Sánchez-Noguera, Álvaro Morales-Ramírez, Christian Wild

Effects of simulated overfishing on the succession of benthic algae and invertebrates in an upwelling-influenced coral reef of Pacific Costa Rica

This study was initiated by I. Stuhldreier, F. Roth, and C. Wild. The experimental work was designed by F. Roth with the support of I. Stuhldreier and C. Wild. Data acquisition was conducted by F. Roth, I. Stuhldreier and C. Sánchez-Noguera. The data was analyzed by F. Roth and the manuscript was written by F. Roth with support of all authors. This article has been published in Journal of Experimental Marine Biology and Ecology 468: 55-66 (2015).

Publication 5

Christian Wild, Tim Rixen, Celeste Sánchez-Noguera, Ines Stuhldreier, Carlos Jiménez, Agostino Merico

Massive coral tissue ablations in reefs of Pacific Costa Rica

This manuscript, which describes an interesting observation at the study site, was written by C. Wild with support of all authors. This article has been published in Galaxea, Journal of Coral Reef Studies 16: 13-14 (2014).

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2 Seasonal upwelling controls organic matter cycles above eastern tropical Pacific coral reefs

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Abstract

The Gulf of Papagayo at the northern Pacific coast of Costa Rica experiences pronounced seasonal changes in water parameters caused by wind-driven coastal upwelling. While remote sensing and open water sampling described the physical nature of this upwelling, the spatial and temporal effects on key parameters and processes in the water column have not been investigated yet, although being highly relevant for coral reef functioning. The present study investigated a range of water parameters above two coral reefs with different exposure to upwelling (Matapalo and Bajo Rojo) in a weekly to monthly resolution over one year (May 2013 to April 2014). Based on air temperature, wind speed and water temperature, three time clusters were defined: a) May to November 2013 without upwelling, b) December 2013 to April 2014 with moderate upwelling, punctuated by c) extreme upwelling events in February, March and April 2014. During upwelling peaks, water temperatures decreased by 7 °C (Matapalo) and 9 °C (Bajo Rojo) to minima of 20.1 and 15.3 °C respectively, while phosphate, ammonia and nitrate concentrations increased 3- to 16-fold to maximum values of 1.3 µmol PO_4^{3-} L^{-1}, 3.0 µmol NH_4^+ L^{-1} and 9.7 µmol NO_3^- L^{-1}. This increased availability of nutrients triggered several successive phytoplankton blooms as indicated by 3- (Matapalo) and 6-fold (Bajo Rojo) increases in chlorophyll *a* concentrations. Particulate organic carbon and nitrogen (POC and PON) increased by 40 and 70 % respectively from February to April 2014. Dissolved organic carbon (DOC) increased by 70 % in December and stayed elevated for at least 4 months, indicating high organic matter release by primary producers. Such strong and long-lasting influences on chlorophyll *a* and organic matter concentrations above coral reefs have not been reported previously. Organic matter cycles above coral reefs in the Gulf of Papagayo are primarily controlled by seasonal upwelling.

2.1 Introduction

Coral reefs require warm, sunlit, clear, oligotrophic and carbonate-supersaturated conditions for optimal growth (Kleypas et al. 1999). Sedimentation and turbidity, nutrient availability, amounts and types of organic matter in the water, contaminants, salinity, temperature and alkalinity can all strongly influence the productivity, resilience and function of coral reef ecosystems (Fabricius 2005). While coral reef environments are generally characterized by a high degree of stability (Hoegh-Guldberg 1999), higher instability of conditions is projected for future coral reefs, as global stressors such as ocean warming and acidification along with local pressures such as eutrophication and pollution from land are increasing (Selman et al. 2008, Pandolfi et al. 2011). The potential of coral reefs to adapt to these environmental changes is still under debate (Berkelmans & van Oppen 2006, Hoegh-Guldberg 2011). Some reefs existing in areas exposed to high natural variations in water quality may serve as natural laboratories to study the effects of changes in environmental parameters on coral reef functioning. Reefs along the Pacific coast of Mesoamerica for instance are exposed to highly dynamic water conditions in space and time. The Eastern Pacific Warm Pool with sea surface temperatures above 27 °C is interrupted by seasonal coastal upwelling zones in the gulfs of Tehuantepec (Mexico), Papagayo (Costa Rica - Nicaragua), and Panama (Panamá) (McCreary et al. 1989, Kessler 2006). These upwelling systems are caused by narrow wind jets blowing from land to sea during the northern hemisphere winter, when high pressure systems in the Caribbean promote strong winds that are canalized through topographical gaps in the volcanic mountain range of Mesoamerica (Legeckis 1988, Amador et al. 2006). In response to wind forcing, shallow water currents in the Pacific displace superficial water away from the coast, causing an uplift of the shallow thermocline (D'Croz & O'Dea 2007). In combination with intense vertical mixing by high wind speeds, this phenomenon brings water with low temperature, low pH and high concentrations of nutrients to the surface between November and April (Lavín et al. 2006). In the Gulf of Papagayo, temperatures of 10 °C below the annual mean and down to <15 °C have been measured during upwelling months (Legeckis 1988, Jiménez 2001, Alfaro & Cortés 2012), and drops in pH from 8.01 to 7.86 units within 30 minutes were recorded during upwelling events (Rixen et al. 2012). In the Gulf of Panama, nutrient concentrations up to 14.5 µmol L^{-1} nitrate and 1.2 µmol L^{-1} phosphate were measured during upwelling season (D'Croz & O'Dea 2007).

Low temperatures, high nutrient concentrations and the fast changes in these key water parameters are unfavorable for coral growth. However, coral communities and reefs occur along the northern Pacific coast of Costa Rica despite the occurrence of seasonal upwelling (Cortés & Jiménez 2003). So far it is known that the northern Pacific coast of Costa Rica experiences strong seasonal variations in oceanographic parameters, but this information

derives from remote sensing or sampling of the open water column. The spatial and temporal effects of upwelling on organic parameters and processes in the water column which are relevant for coral reef functioning have not been investigated yet. Therefore, this study monitored temporal variability of temperature, salinity, pH, oxygen availability, nutrients and chlorophyll *a* concentrations as well as particulate and dissolved organic matter. Monitoring was conducted on two coral reefs differently exposed to upwelling in a weekly to monthly temporal resolution over a period of 12 months. The goal was to describe how long and to what extent the key water column parameters mentioned above are influenced by seasonal upwelling. In contrast to oceanographic data from previous studies, the data presented here illustrate fine-scale trends and processes in reef waters in the Gulf of Papagayo.

2.2 Material and Methods

2.2.1 Study sites

Water conditions were monitored at two reef sites in the Gulf of Papagayo, situated in 46.3 km air-line distance to each other (Fig. 2.1). Matapalo reef is dominated by the branching coral *Pocillopora* spp. and extends around 1 km along the northern coast of the Nicoya Peninsula, with alternating patches of dead and living carbonate structure in 3 - 8 m water depth. An area of around 600 m^2 with relatively high live coral cover compared to the surrounding area was visited weekly. North of the Santa Elena Peninsula the upwelling is stronger, because the trade wind flow from the Caribbean during the northern hemisphere winter is not blocked by the volcanic mountain range of Central America (Fig. 2.1). The study site Bajo Rojo is a small rocky outcrop 2 km off the coast, where a reef dominated by *Pavona gigantea* stretches around 70 m along the base of the rock in 7 - 11 m water depth. This site was visited monthly. Data from Matapalo are discussed in detail, while data from Bajo Rojo are described in relation to Matapalo. Necessary field permits were granted by the National System of Conservation Areas (SINAC) of Costa Rica.

2.2.2 Seasonal periods

The 12 month study period from 01 May 2013 to 21 April 2014 encompassed the rainy season from May to November, and the dry trade-wind season from December to April. The transitions between these seasons are not well defined, and periods may vary between years. For this study, we defined time periods using a multivariate clustering routine in PRIMER 6 based on similarity in air temperature, wind speed and water temperature between 15 April 2013 and 21 April 2014. Meteorological data (Fig. 2.2) originated from the Daniel Oduber Quirós International Airport station (10°35'35"N, 85°32'44"W, 80 m above

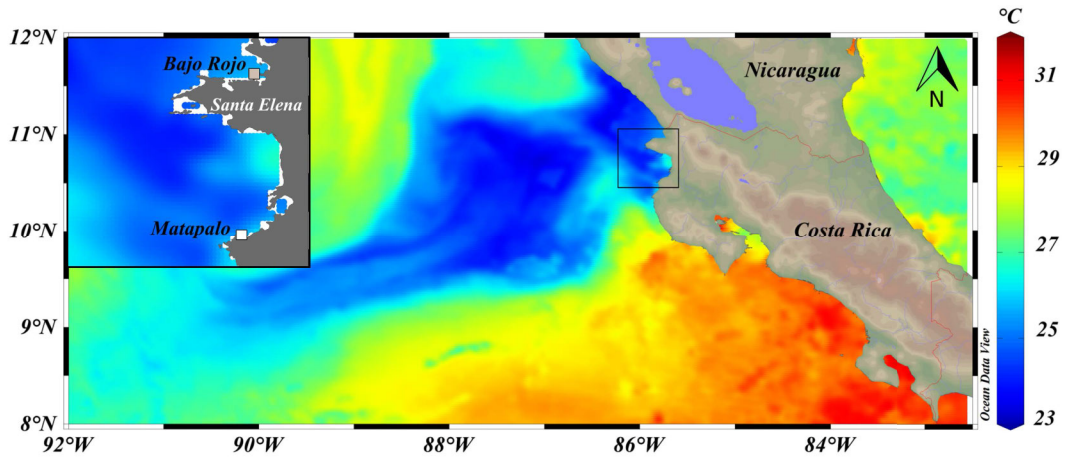

Figure 2.1: Upwelling event off the Pacific coast of Costa Rica on 17 February 2014. Color scale in the water indicates sea surface temperature (SST). Shading on land indicates altitude; note the depression in the volcanic mountain range at Lake Nicaragua that enables Trade Wind crossing from the east. The inset shows the locations of study sites Matapalo (10°32'21"N, 85°45'59"W) and Bajo Rojo (10°57'26"N, 85°43'59"W). Data were derived from a daily, global 1-km SST data set (GHRSST, Level 4, G1SST) produced by the JPL OurOcean group (Chao et al. 2009) and visualized with the software Ocean Data View (Schlitzer, R., Ocean Data View, http://odv.awi.de, 2013).

sea level), 25 km northeast of Matapalo and 45 km southeast of Bajo Rojo, and daily averages were obtained from http://www.ncdc.noaa.gov/cdo-web/datasets (accessed July 2014). Water temperature was measured in 5 m depth at Matapalo in 5-30 min intervals (see below) and calculated to daily averages. The cluster analysis (resemblance based on Euclidean distance, complete linkage) resulted in three groups: a) non-upwelling period (noUPW) including 215 days mainly from May to November 2013, b) upwelling period (UPW) including most days in April 2013, some days over the year and most days from December 2013 to April 2014 and c) extreme upwelling (extUPW) including 15 days in February, March and April 2014. Based on this analysis, the days of weekly/monthly sampling were assigned to their respective cluster ($n_{noUPW} = 34$, $n_{UPW} = 20$, $n_{extUPW} = 5$) which was later used as a factor to determine the differences in environmental parameters between seasons.

2.2.3 Monitored parameters

Water temperature was recorded continuously at both study sites with HOBO® Pendant Temperature Data loggers deployed directly above the reef substrate. Intervals were 30 min during non-upwelling, 10 or 15 min (Matapalo and Bajo Rojo respectively) from December to beginning of February and 5 min during upwelling season. Due to loss and malfunction of loggers, there are no data available for Bajo Rojo from 12 Sept 2013 to 12 Nov 2013 and from 20 Nov 2013 to 10 Dec 2013.

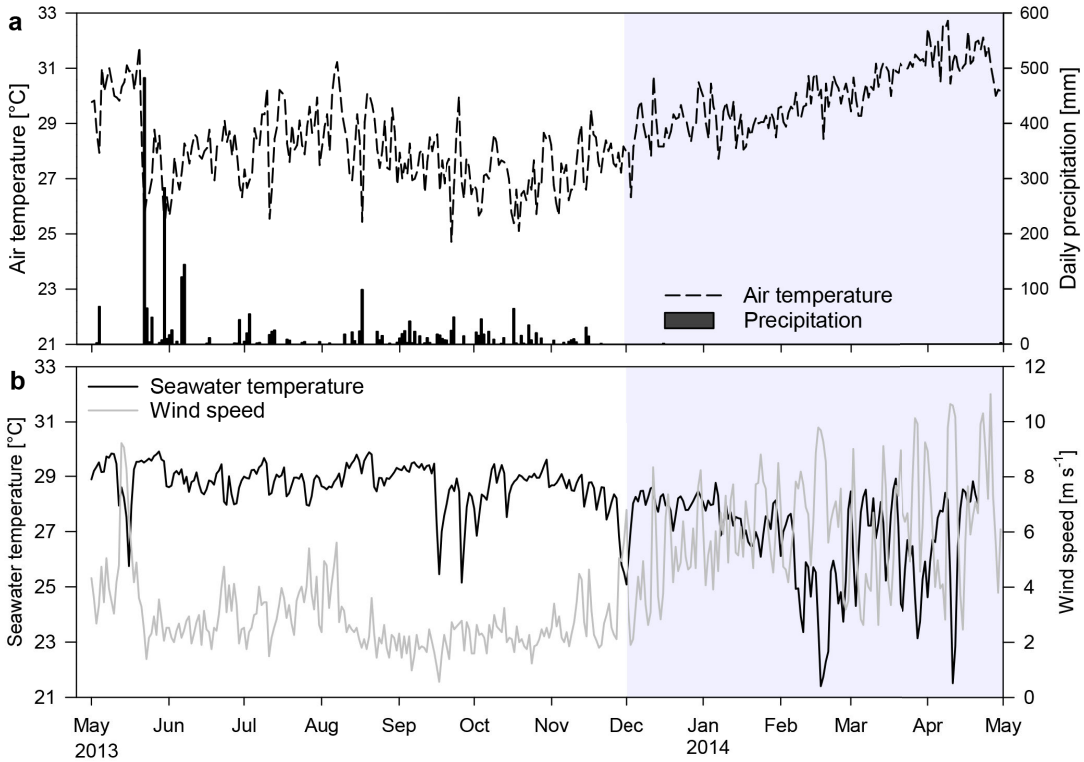

Figure 2.2: Changes in meteorological parameters and seawater temperature in 5 m depth at Matapalo over 12 months. (a) Mean daily air temperature [°C] and daily precipitation [mm]. (b) Mean daily seawater temperature [°C] and mean daily wind speed [m s^{-1}]. Shaded area = upwelling period.

Salinity, oxygen concentration and pH were recorded in 4 min intervals with a Manta 2 Water Quality Multiprobe by placing the multisensor directly on the reef substrate (distance sensors to reef structure around 10 cm) for 1 - 7 hours during weekly/monthly observations. Additionally, temporal profiles over 7 days were recorded bi-weekly between December 2013 and April 2014 at Matapalo to correlate water parameters to each other during upwelling season. We corrected pH data for temporal shifts in sensor readings, and for logger specific differences.

2.2.4 Water analyses

Water for the determination of dissolved organic carbon (DOC) and inorganic nutrient concentrations was sampled in triplicates from directly above the reef substrate (10 - 20 cm distance) in seawater washed 500 mL glass jars closed with glass lids. Directly after the dive, samples were filtered and stored cool for transportation. All syringes and containers were pre-washed twice with the respective sample, and powder-free gloves were used to avoid contamination. For DOC analysis, samples were filtered through pre-combusted

glass microfiber filters (VWR, 25 mm, particle retention 0.7 µm) in polycarbonate syringe-filter-holders into new 30 mL HDPE wide-neck bottles and frozen within 3 h after sampling. For analysis, samples were defrosted, acidified with 28 µL 33 % HCl per 30 mL sample, to reach pH ≤ 2, and analyzed in a Shimadzu TOC-VCPH + TNM1 + ASI-V elemental analyzer. Samples were analyzed for Non Purgeable Organic Carbon (NPOC) using high temperature combustion (720 °C) and detection of CO_2 by a non-dispersive infrared detector conforming to U.S. EPA Method 415.1 (U.S. Environmental Protection Agency 1983). Samples for inorganic nutrient concentrations were filtered through disposable syringe filters (pore size 0.45 µm) into darkened 15 mL glass (for ammonia NH_4^+ and phosphate PO_4^{3-}) or new 50 mL polypropylene containers (for nitrate NO_3^- and nitrite NO_2^-). NH_4^+ was determined fluorimetrically within 24 h after sampling with a Trilogy® Laboratory Fluorometer/Photometer (Turner Designs) after overnight incubation with OPA (orthophthaldialdehyde)-solution in the dark (Holmes et al. 1999, Taylor et al. 2007). All other samples were frozen within 3 h after sampling. Determinations of PO_4^{3-} were conducted spectrophotometrically with the same device at 880 nm (Murphy & Riley 1962). Samples in polypropylene containers were kept dark and frozen until the end of the study period and were analyzed for NO_3^- and NO_2^- concentrations using a photometer (Thermo Scientific UV Evolution 201®) at 543 nm after reduction of NO_3^- to NO_2^- with vanadium (III) (García-Robledo et al. 2014).

Samples for the determination of chlorophyll *a* (chl *a*) and particulate organic matter (POM) concentrations were taken in triplicate in 3.8 L pre-washed plastic bottles from 20 cm below the sea surface over the reef at the end of weekly/monthly visits. Within 3 h after sampling, subsamples of each container (1 L for chl *a*, 2 L for POM after gentle agitation of containers) were filtered onto VWR glass microfiber filters (47 mm, particle retention 1.6 µm) with an electric vacuum pump (max. pressure <200 mbar). Filters for POM were pre-combusted, pre-weighed and stored in combusted tinfoil. Directly after filtration, chl *a* filters were homogenized in 7 mL 90 % acetone with a glass rod, and the filter slurry was incubated overnight at 4 °C. Samples were centrifuged for 10 min at 805 g before an aliquot of the supernatant was transferred to a glass cuvette. Fluorescence was measured with the Trilogy® Laboratory Fluorometer/Photometer before and after acidification to 0.003 N HCl with 0.1 N HCl for 90 seconds. Procedure and calculations were carried out according to U.S. EPA Method 445.0 (Arar & Collins 1997). The filters for the POM analysis were kept frozen at -20 °C until the end of the study period, then dried for 24 h at 40 °C and weighed with a digital scale (precision 0.001 g) to calculate the amount of particulate matter (PM) in seawater. Dried filters were thereafter analyzed for total carbon (C), nitrogen (N) and organic carbon (C_{org}) content in a CHN elemental analyzer (Eurovector Euro EA 3000). A quarter of the filter was used for i) the determination of C and N in tin-cups and ii) C_{org} in silver-cups after acidification with 200 µL 1 N HCl.

2.2.5 Statistical analysis

If not stated otherwise, data are always displayed as means ± standard error (SE). Statistical analyses were performed with weekly/monthly data points of environmental variables resulting in n = 59 independent samples for each of the 10 variables. Analyses of chl *a*, DOC, POC and PON did not start before July 2013. Missing values (n = 9 for chl *a*, n = 11 for DOC, n = 8 for POC and PON, n = 4 for NO_3^-) were substituted by average values of the same parameter from the same site between May and October 2013 to enable statistical analyses of multivariate PERMANOVAs and Principal component ordination (PCO).

The effects of Season (nonUPW, UPW, extUPW) and Site (Matapalo, Bajo Rojo) were examined on i) all water parameters, ii) physicochemical water parameters (salinity, pH, oxygen), iii) inorganic nutrients (PO_4^{3-}, NH_4^+, NO_3^-), and iv) organic parameters (chl *a*, DOC, PON, POC) by permutation multivariate analyses of variance (PERMANOVA) (Anderson 2001, Anderson et al. 2008) in PRIMER 6, followed by pair-wise comparisons among seasons by additional post hoc PERMANOVA routines. Prior to analysis, inorganic nutrients and organic parameters were log(x+1) transformed to meet the requirements of Gaussian distribution and to scale down the effects of extreme outliers. Additionally, univariate ANOVAs with subsequent Tukey Tests were performed for each environmental variable and factor separately in R 3.1.1 (function aov and TukeyHSD). Inorganic nutrients and organic parameters were log transformed prior to analysis to meet requirements of Gaussian distribution. Thereafter, environmental variables were normalized and a resemblance matrix was calculated based on Euclidean similarity. Principal coordinate ordinations (PCO) (Gower 1966) were used to ordinate the multivariate data based on similarities in all measured water parameters in order to visualize the difference between seasons and sites.

2.3 Results

2.3.1 Effects of Season and Site

Multivariate analyses showed significant differences between seasons (non-upwelling, upwelling, extreme upwelling) and sites (Matapalo, Bajo Rojo) for i) all water parameters, ii) physicochemical water parameters (salinity, pH, oxygen), iii) inorganic nutrients (PO_4^{3-}, NH_4^+, NO_3^-), and iv) organic parameters (chl *a*, DOC, PON, POC). Season, Site and all pair-wise test were p <0.010 except the comparison of noUPW to UPW in inorganic nutrients (p = 0.039) and UPW to extUPW in organic parameters (p = 0.035). The only non-significant term was the comparison of UPW and noUPW in physicochemical parameters. Subsequent univariate analysis confirmed seasonal differences in all parameters except dissolved oxygen, chlorophyll *a* and POC. The differences in single parameters were mostly detected between extUPW and noUPW (all except DOC), but also between extUPW and UPW (pH,

PO_4^{3-}, NO_3^-), and between noUPW and UPW (pH, PO_4^{3-}, DOC). Principal coordinate ordinations visualized the seasonal pattern among all environmental variables for the Gulf of Papagayo, which is consistent with the results from multivariate PERMANOVA analyses (Fig. 2.3). The first PCO axis of the model explained 39.6 % of the data variation and showed a highly significant correlation (coefficients ≥ 0.80) with PO_4^{3-} and NO_3^- and further correlations (coefficients ≥ 0.50) with salinity, oxygen, NH_4^+, chl *a*, PON and POC. The second PCO axis explained another 15.5 % of the data variation correlating with pH, oxygen, and DOC (coefficients ≥ 0.50). According to their (dis)similarity in Euclidean distance, data during extreme upwelling events in February and March were clearly separated from non-upwelling period (May-Nov), whereas upwelling (Dec-Apr) was overlapping with both other groups, indicating that the time clusters based on temperatures and wind speed are not clearly mirrored in measured water parameters.

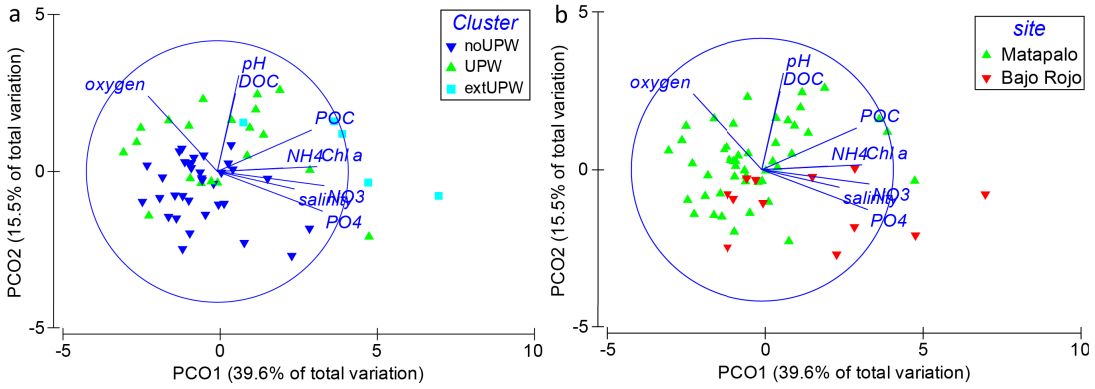

Figure 2.3: Graphical representation of multivariate analyses results by principal coordinates ordination (PCO). Data of environmental variables were grouped by (a) upwelling period (*noUPW* non-upwelling, *UPW* upwelling, *extUPW* extreme upwelling) and (b) site (Matapalo, Bajo Rojo). Effects and directions of environmental variables are displayed as vectors (abbreviations in italic): salinity, pH, oxygen, PO_4^{3-} phosphate, NH_4^+ ammonia, NO_3^- nitrate, *Chl a* chlorophyll *a*, *POC* particulate organic carbon (also represents *PON* particulate organic nitrogen), *DOC* dissolved organic carbon.

2.3.2 Temporal variability of water parameters at Matapalo Reef

From May 2013 to April 2014, Matapalo reef experienced high variability in temperature (20.1 - 30.6 °C), salinity (30.6 - 34.3), pH (7.83 - 8.38), oxygen (4.2 - 9.1 mg L^{-1}), phosphate (0.04 - 1.30 µmol L^{-1}), ammonia (0.22 - 2.53 µmol L^{-1}), nitrate (below detection limit - 6.74 µmol L^{-1}), chlorophyll *a* (0.11 - 2.22 µg L^{-1}), POC (95.3 - 726.9 µg L^{-1}), PON (13.1 - 118.8 µg L^{-1}) and DOC (77.5 - 293.6 µmol L^{-1}). Average values for each seasonal period are displayed in Table 2.1.

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Table 2.1: Mean environmental parameters (± SE) at Matapalo Reef in 5 m water depth during the three main seasonal periods (defined by cluster analysis, see 2.2.2)

Water column Matapalo	non-upwelling nUPW	upwelling UPW	extreme upwelling extUPW
Temperature [°C]	28.7 ± 0.1 (215)	27.4 ± 0.1 (142)	23.2 ± 0.3 (15)
pH	8.02 ± 0.01 (26)	8.08 ± 0.02 (15)	8.28 ± 0.01 (4)
Salinity	32.56 ± 0.18 (26)	32.86 ± 0.29 (15)	33.80 ± 0.14 (4)
Dissolved O_2 [mg L^{-1}]	7.07 ± 0.14 (26)	7.19 ± 0.09 (15)	6.27 ± 0.48 (4)
Phosphate [µM]	0.28 ± 0.02 (26)	0.20 ± 0.04 (15)	0.77 ± 0.20 (4)
Ammonia [µM]	0.59 ± 0.05 (26)	0.65 ± 0.09 (15)	1.39 ± 0.41 (4)
Nitrate [µM]	0.47 ± 0.06 (24)	0.37 ± 0.11 (15)	3.55 ± 1.21 (4)
Chlorophyll *a* [µg L^{-1}]	0.59 ± 0.08 (19)	0.68 ± 0.11 (15)	1.20 ± 0.50 (4)
Particulate N [µg L^{-1}]	27.22 ± 2.54 (20)	42.06 ± 8.35 (15)	57.48 ± 12.26 (4)
Particulate organic C [µg L^{-1}]	226.88 ± 28.53 (20)	292.78 ± 49.50 (15)	327.68 ± 51.62 (4)
Dissolved organic C [µM]	110.98 ± 7.25 (18)	184.43 ± 13.37 (15)	137.31 ± 11.33 (4)

Variables were measured constantly (water temperature; daily averages), weekly for several hours (pH, salinity, dissolved O_2; sampling day average) or weekly in triplicate (nutrients and particulate as well as dissolved organic matter; sampling day average). The number of replicates for each parameter and season is displayed in brackets.

Physicochemical parameters

The non-upwelling season from May to November 2013 was characterized by high and stable sea surface temperatures. However, pronounced but short drops to 24.4 °C were observed in May and September 2013, lasting 2-5 days. These drops in temperature followed days with unusually high wind speeds, except two cold water intrusions in September 2013, when no elevated wind speeds were recorded (Fig. 2.2b). After a first upwelling event in December 2013, temperatures returned to around 28 °C before dropping down to 23.4 °C in February 2014. Over the following three months, mean daily seawater temperatures dropped repeatedly by 2.2 to 6.8 °C to minimum daily averages of 21.4 °C for 4 - 6 days, after which temperatures returned to 26 - 29 °C (Fig. 2.4a). Salinity experienced a seasonal pattern independent of upwelling. Lowest salinities of 30.6 occurred in December 2013, but quickly increased to ≥ 33.0 with the beginning of dry season. Maximum salinities of 34.2 in February were associated with upwelling events (Fig. 2.4a). Salinity was negatively correlated to seawater temperature during upwelling season (r = -0.59, n = 4730, p <0.001). The reef water was usually very well oxygenated with saturation states of around 95 %, despite occasional concentrations below 3 mg O_2 L^{-1} during night-time. Two drops in oxygen concentrations to 4.6 mg O_2 L^{-1} during day-time were associated with cold water temperatures, but average concentrations did not decrease significantly during upwelling season

(Fig. 2.4b). However, minimum values in the early morning were significantly decreased during upwelling (4.37 ± 0.11 mg O_2 L^{-1}) compared to non-upwelling season (4.73 ± 0.08 mg O_2 L^{-1}; t = 2.26, df = 71, p = 0.027). Values of pH were significantly higher in upwelling season compared to non-upwelling and highest in February when upwelling was strongest (Fig. 2.4b). Oxygen concentration and pH experienced strong daily oscillations with lowest values during early morning hours and highest values during midday. Oxygen concentrations varied between 4.51 ± 0.08 and 7.92 ± 0.08 mg L^{-1} O_2 (n = 73), and pH between 7.87 ± 0.01 and 8.02 ± 0.01 units (n = 47) within 24 hours. Correlation of O_2 and pH on a daily cycle was highly significant (r = 0.63, n = 2893, p <0.001).

Inorganic nutrients

Inorganic nutrient concentrations were low and stable during non-upwelling and upwelling season despite occasional drops in temperature. They increased significantly by 260 % (PO_4^{3-}), 190 % (NH_4^+) and 690 % (NO_3^-) during extreme upwelling events, reaching maximum values of 1.3 µmol PO_4^{3-} L^{-1}, 2.5 µmol NH_4^+ L^{-1} and 6.7 µmol NO_3^- L^{-1} during the strongest recorded upwelling event on 17 February 2014 (Fig. 2.4c). Nitrite concentrations stayed very low during the whole year and are therefore not shown in the following.

Organic parameters

Chlorophyll *a* concentrations were 2-fold higher during extreme upwelling compared to upwelling and non-upwelling season. Concentrations peaked once in December and several times between February and April, thereby increasing from an average of 0.6 µg chl *a* L^{-1} to maximum values of up to 2.2 µg chl *a* L^{-1} (Fig. 2.4d). While inorganic nutrient concentrations decreased after March 2014, chl *a* stayed elevated at around 1 µg L^{-1} until the end of April. Particulate organic carbon (POC) and nitrogen (PON) in the water column increased temporary after a short upwelling event in December, and more persistent in March and April 2014, resulting in 40 % (POC) and 80 % (PON) higher values in upwelling compared to non-upwelling season (Fig. 2.4e). While inorganic nitrogen, represented by NO_3^- and NH_4^+, decreased after March, organic nitrogen in the form of PON stayed elevated for at least 3 more weeks, until the end of the sampling period. Between February and April 2014, the reef experienced approximately 39 and 46 % of the annual POC and PON production. Dissolved organic carbon (DOC) increased by 70 % two weeks after the first short upwelling event in December and stayed elevated for the following 4 month. Peaks in DOC followed elevations in chlorophyll *a* and POC/PON concentrations with a delay of 2 - 4 weeks.

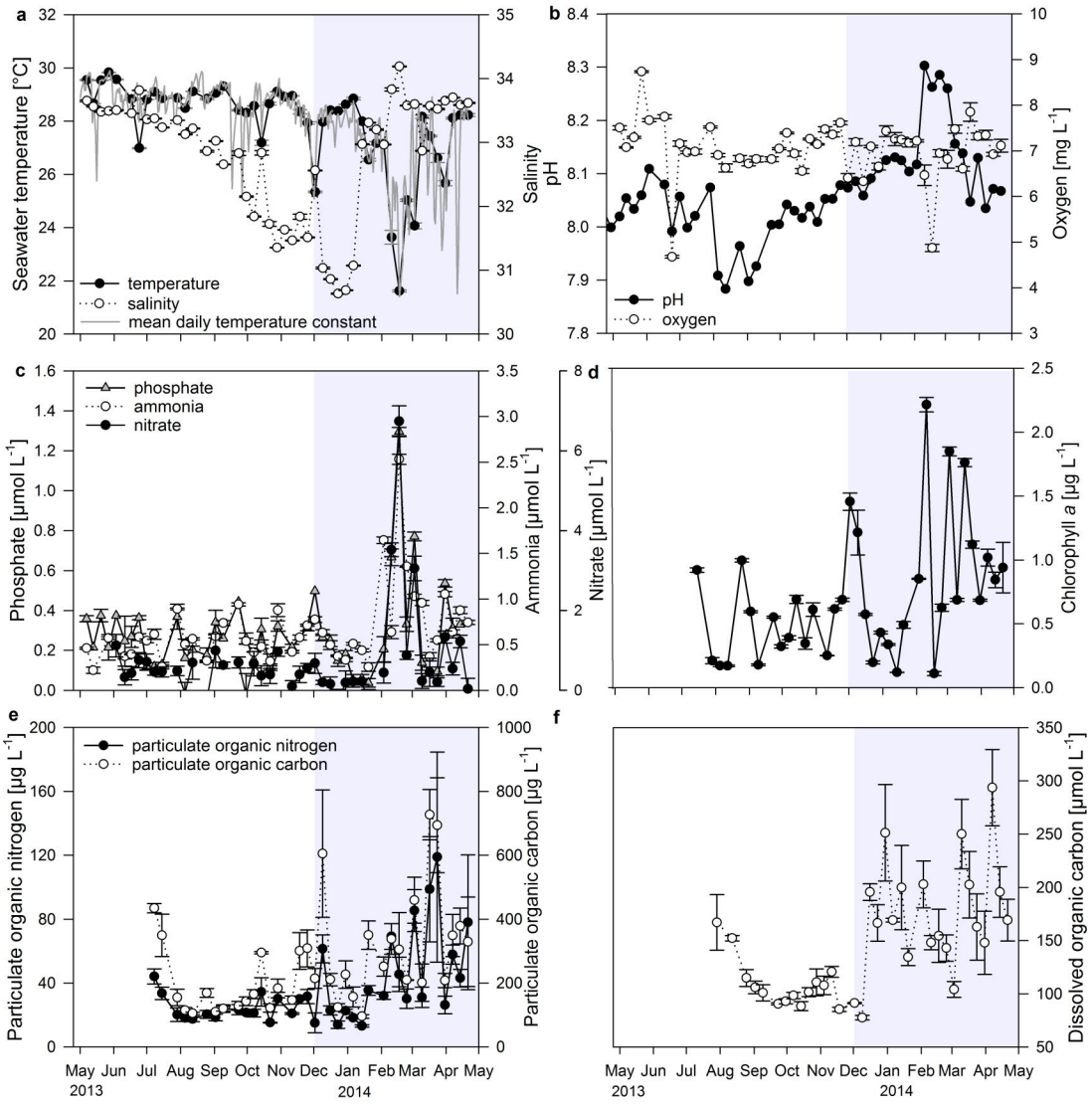

Figure 2.4: Changes in environmental parameters at Matapalo in a weekly resolution over 12 months. (a) Seawater temperature and salinity; (b) pH value and concentration of dissolved oxygen in the water column; (c) inorganic nutrient concentrations for phosphate, ammonia and nitrate; (d) concentration of chlorophyll *a*; (e) particulate organic nitrogen and carbon in the water column; (f) concentration of dissolved organic carbon. Error bars indicate ± SE. Shaded area = upwelling period.

2.3.3 Comparison between sites Matapalo and Bajo Rojo

Water parameters at Bajo Rojo followed a similar seasonal pattern as those at Matapalo (Table 2.2). Univariate analyses showed significant differences between sites in all physico-chemical parameters, but not in inorganic nutrients or organic parameters except PO_4^{3-} and chl *a*.

Table 2.2: Mean environmental parameters (± SE) at Bajo Rojo Reef in 10 m water depth during the three main seasonal periods (defined by cluster analysis, see 2.2.2).

Water column Matapalo	non-upwelling nUPW	upwelling UPW	extreme upwelling extUPW
Temperature [°C]	27.3 ± 0.1 (134)	23.5 ± 0.2 (124)	18.8 ± 0.4 (15)
pH	7.95 ± 0.02 (7)	7.98 ± 0.06 (4)	8.03 (1)
Salinity	33.18 ± 0.24 (7)	33.72 ± 0.22 (4)	34.70 (1)
Dissolved O_2 [mg L^{-1}]	5.76 ± 0.41 (7)	5.87 ± 0.40 (4)	5.61 (1)
Phosphate [µM]	0.36 ± 0.06 (7)	0.48 ± 0.03 (4)	1.21 (1)
Ammonia [µM]	0.47 ± 0.15 (7)	1.32 ± 0.57 (4)	0.47 (1)
Nitrate [µM]	0.31 ± 0.17 (7)	2.66 ± 1.68 (4)	9.71 (1)
Chlorophyll *a* [µg L^{-1}]	0.98 ± 0.47 (7)	1.24 ± 0.46 (4)	7.71 (1)
Particulate N [µg L^{-1}]	35.96 ± 5.20 (7)	49.41 ± 10.78 (4)	89.45 (1)
Particulate organic C [µg L^{-1}]	276.47 ± 35.56 (7)	326.21 ± 83.39 (4)	658.01 (1)
Dissolved organic C [µM]	102.46 ± 1.72 (7)	162.39 ± 29.05 (4)	141.71 (1)

Variables were measured constantly (water temperature; daily averages), weekly for several hours (pH, salinity, dissolved O_2; sampling day average) or weekly in triplicate (nutrients and particulate as well as dissolved organic matter; sampling day average). The number of replicates for each parameter and season is displayed in brackets.

Physicochemical parameters

From May to November 2013, mean daily water temperatures in Bajo Rojo were on average 1.6 ± 0.1 °C lower and more variable than in Matapalo. During upwelling, Bajo Rojo experienced on average 4.1 ± 0.2 °C lower mean daily temperatures than Matapalo, and water temperatures dropped to a minimum of 16.0 °C (Fig. 2.5a). To ensure that these temperature differences were not due to differences in water depth, temperature data from Matapalo were compared with data from a shallow reef (3 m water depth) close to Bajo Rojo. At this shallow reef, water temperature was still significantly lower than at Matapalo (U = 19836, n = 250, p <0.001) and dropped to 18.4 °C in upwelling season, thereby confirming a north-south gradient in upwelling intensity, independent of water depth. Mean daily water temperatures at Bajo Rojo and Matapalo were highly correlated to each other over the entire year (r = 0.877, n = 272, p <0.001). During non-upwelling season, drops in temperature often occurred first in Bajo Rojo and were measured with a delay of about two days in Matapalo, whereas stronger upwelling events between February and April occurred simultaneously at both sites. Salinity in Bajo Rojo displayed the same temporal pattern as in Matapalo, with lowest values of 32.6 in December and increases in the upwelling season (Fig. 2.5b). Water oxygen concentrations and pH at Bajo Rojo were on average lower than in Matapalo, with values ranging from 4.0 to 7.1 mg O_2 L^{-1} and a pH of 7.75 to 8.10 units (Fig. 2.5c and d).

Inorganic nutrients and organic parameters

Similar to Matapalo, PO_4^{3-} and NO_3^- concentrations peaked in February (1.2 ± 0.1 and 9.7 ± 0.4 µmol L^{-1} respectively) and were associated with highest chl *a* values (7.7 ± 0.3 µg L^{-1}), whereas NH_4^+ concentrations were highest in April (3.0 ± 0.1 µmol L^{-1}). Maximum PO_4^{3-} and NH_4^+ concentrations were similar to Matapalo, while maximum concentrations of NO_3^- and chl *a* were 1.4 and 3.5 times higher at Bajo Rojo (Fig. 2.5e-h). Particulate and dissolved organic matter concentrations at Bajo Rojo were in the same range than at Matapalo, experiencing similar temporal patterns with higher values during upwelling season (Fig. 2.5i-k).

2.4 Discussion

2.4.1 Temporal variability of water parameters

In the Gulf of Papagayo, changes in temperature and nutrient concentrations occurred in pulses during a major upwelling period from February to April. These changes in water parameters were more pronounced at the northern site, confirming the proposed gradient in upwelling intensity.

Physicochemical parameters

Drops in seawater temperature of 2 - 9 °C for several days indicated a pronounced influence of upwelling at the study sites, although the effect on temperature was smaller and/or shorter compared to areas in Thailand (5 - 9 °C, Schmidt et al. 2012) and in Caribbean Colombia (5 months, Bayraktarov et al. 2014). The upwelling at the study sites increased surface salinities to over 34, thereby interrupting the low salinity zone beneath the Inter-Tropical Convergence Zone in the eastern tropical Pacific, where precipitation exceeds evaporation and salinities are usually below 33 (Fiedler & Talley 2006). Seasonal variability in salinity was therefore high, but still within the environmental limits for corals (25 - 42, Kleypas et al. 2001). Similar variability in salinity was already observed in other upwelling areas in the Gulf of Panama (29.2 - 33.6, D'Croz & O'Dea 2007) and in Caribbean Colombia (32.5 - 39.0, Bayraktarov et al. 2014). The observed semidiurnal variations in oxygen concentrations and pH in the study area were similar to tropical reef systems in Florida (1.7 - 3.0 mg O_2 L^{-1}, Yates et al. 2007) or French-Polynesia (0.10 - 0.25 pH units, Hofmann et al. 2011) and can be related to diurnal changes in biological processes such as photosynthesis and respiration (Smith & Key 1975, Shaw et al. 2012). On a seasonal scale, pH values were highest in February 2014 during strongest upwelling. In contrast, pH decreased 0.6 units during cold-water intrusions in the Similan Islands (Schmidt et al. 2012) and 0.15 units in Papagayo Bay associated with a short upwelling event (Rixen et al. 2012). Surface waters usually

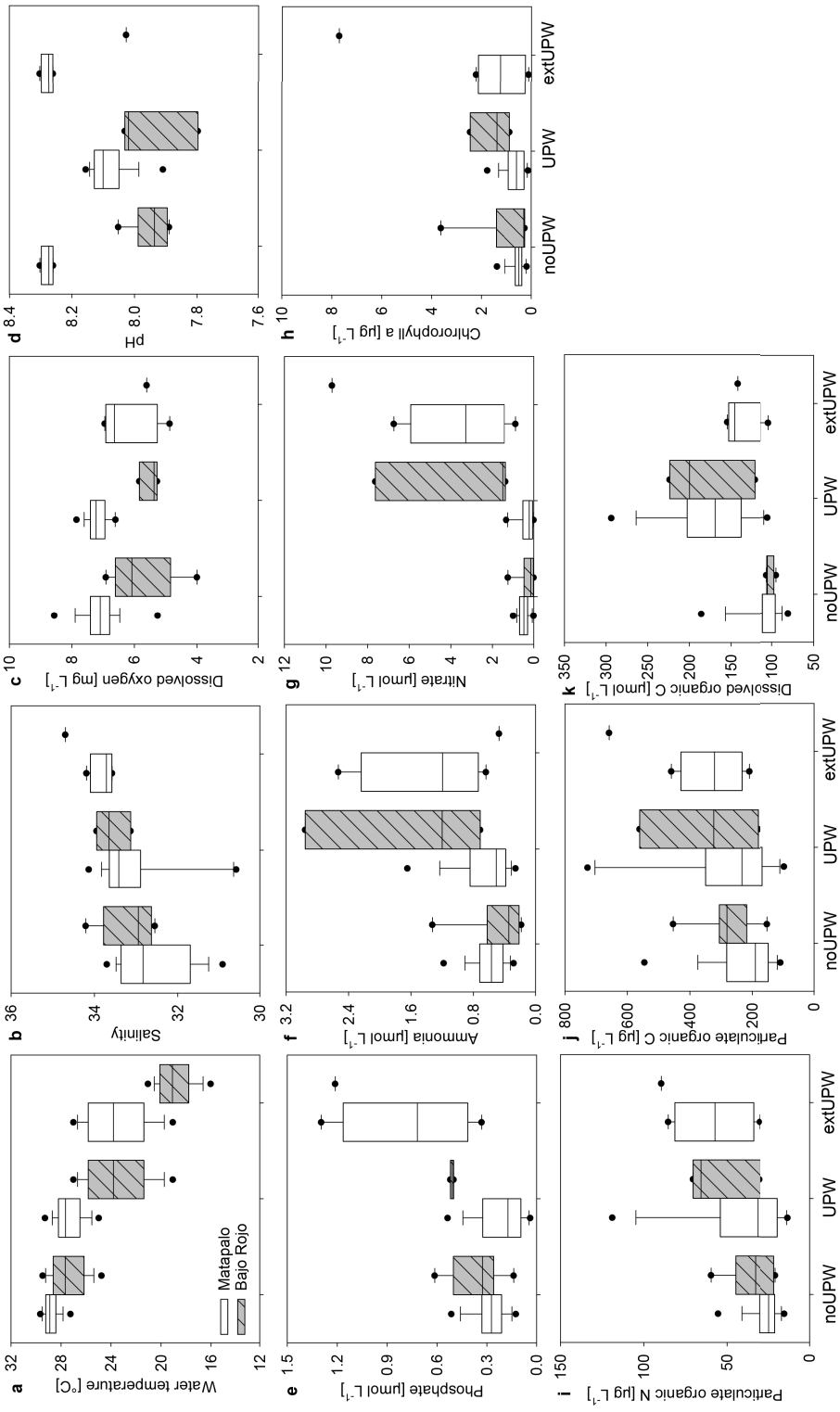

Figure 2.5: Differences in water parameters comparing Matapalo (medium exposed) and Bajo Rojo (highly exposed to upwelling). Displayed group medians were calculated from weekly (Matapalo) or monthly (Bajo Rojo) samples. The time periods (*noUPW* non-upwelling, *UPW* upwelling, *extUPW* extreme upwelling) are based on a cluster analysis (see 2.2.2). Box boundaries indicate 25th/75th percentiles; error bars indicate 10th/90th percentiles.

experience a decrease in pH when upwelling processes mix CO_2-enriched deep waters into shallow water layers (Feely et al. 2008, Loucaides et al. 2012). The high pH values recorded during upwelling in the present study may be explained by increased primary productivity in the reef, as chlorophyll *a* concentrations during strongest upwelling events were up to 4-fold higher than average values. The observed oxygen and pH variations therefore suggests that seasonal changes in community metabolism and daily metabolic processes such as photosynthesis and respiration are more important drivers of oxygen and carbonate chemistry variations directly above the reef than upwelling. The reef organisms are thereby able to buffer the upwelling induced changes in oxygen and pH which were observed in the open water column (e.g by Rixen et al. 2012).

Inorganic nutrients

In the present study, concentrations of inorganic nutrients in the reef did not increased during months with high rainfall, indicating that precipitation and runoff were not important sources of nutrients. The delivery of new nutrients to the shallow reefs was therefore primarily controlled by seasonal upwelling. During non-upwelling season, nutrient and chlorophyll *a* concentrations measured in the reef waters were in the upper range of average concentrations in most tropical reefs (3.3 µmol NO_3^- L^{-1}, 0.5 µmol PO_4^{3-} L^{-1}, 0.26 µg chl *a* L^{-1}, Kleypas et al. 1999) and similar to offshore surface data for the Gulf of Papagayo (3.5 µmol NO_3^- L^{-1}, 0.5 µmol PO_4^{3-} L^{-1}, 0.26 µg chl *a* L^{-1}, Pennington et al. 2006). During upwelling, nitrate, phosphate and chlorophyll *a* concentrations increased by 16-, 5- and 4-fold respectively. Comparing measured nutrient and temperature values during upwelling with water depth profiles from oceanographic stations in the Gulf of Papagayo (Pennington et al. 2006), the properties of the upwelling water correspond to those of water from approximately 30-50 m water depth during non-upwelling season, which therefore likely represents the original depth of upwelling water. Maximum nitrate concentrations measured at Matapalo were less than 50 % of the values measured in other eastern Pacific upwelling regions such as Peru (15.0 µmol NO_3^- L^{-1}, Zuta & Guillén 1970) and the Gulf of Panama (14.5 µmol NO_3^- L^{-1}, D'Croz & O'Dea 2007), where water likely wells up from greater water depths.

Organic parameters

During upwelling, high concentrations of nutrients are available which may stimulate primary productivity and phytoplankton growth (Pennington et al. 2006). Accordingly, maximum chlorophyll *a* concentrations in the Gulf of Papagayo occurred in upwelling season, which is concordant with studies in other upwelling areas (D'Croz & O'Dea 2007, Bayraktarov et al. 2014). These maximum concentrations during upwelling were in the same range

than average surface values for the highly productive Peruvian upwelling (2.55 µg chl *a* L^{-1}, Pennington et al. 2006), indicating that the Papagayo upwelling may support productivity similar to one of the most productive upwelling regions of the world, at least for some months of the year. Peaks in chlorophyll *a* in the present study occurred asynchronous with peaks in nutrient concentrations. This suggests rapid uptake of available nutrients by primary producers and a delay in biomass response, as an initial rapid growth of phytoplankton after nutrient addition may take 3 - 5 days (Fawcett & Ward 2011, Malerba et al. 2012). Particulate organic carbon and nitrogen increased together with chlorophyll *a* concentrations, illustrating the conversion of inorganic nutrients into organic matter. The increase in organic matter detected in the present study was much more pronounced than reported from other upwelling areas in the tropics, where concentrations of particulate and dissolved organic matter were similar during non-upwelling, but did not increase during upwelling (Schmidt et al. 2012, Bayraktarov et al. 2014). Organic parameters in this study were elevated much longer than the actual physical upwelling event indicated by temperature and nutrients. This was visible from statistical analyses looking at the non- or weakly significant differences between non-upwelling and upwelling in physicochemical and inorganic parameters respectively (short lived changes in parameters, only visible during extreme upwelling events), whereas the differences in organic parameters were strong between non-upwelling and upwelling season but weak comparing upwelling and extreme upwelling (longer changes in parameters, visible in reef water column for several months). The seasonal upwelling is therefore likely the primary control of organic matter cycles in the studied reefs, and supports around 40 % of the annual production within these three months. Dissolved organic carbon (DOC) in the investigated reefs already increased 2 weeks after the first upwelling event in December and stayed elevated throughout the upwelling season. It is therefore the only measured response parameter that was more extreme in upwelling compared to extreme upwelling period. The increase was likely caused by enhanced photosynthesis and subsequent excess organic matter release by reef organisms such as algae and corals in response to increased nutrient availability after the first upwelling event in December 2013 (Ferrier-Pagès et al. 1998, Haas et al. 2011).

In summary, the effects of upwelling on physicochemical parameters such as temperature and nutrient concentrations were smaller than in comparable upwelling areas. However, such pronounced and long-lasting cascading effects on chlorophyll *a* and organic matter concentrations over the studied reefs have not been reported elsewhere. Significantly increased chlorophyll *a* and organic matter concentrations over periods of 3 months likely have large impacts on local coral reef functioning.

2.4.2 Potential implications for coral reef functioning

Low water temperatures in combination with high nutrient concentrations during upwelling are unfavorable for coral growth. Cold water stress (6 - 10 °C below normal conditions) may disrupt the sensitive association between coral hosts and their endosymbiotic algae and result in decreased fitness, growth, or even bleaching of coral (Coles & Fadlallah 1991, Gates et al. 1992). Accordingly, several studies reported limited coral reef development or coral health in upwelling areas of the eastern tropical Pacific (Glynn et al. 1972, Glynn & Stewart 1973, D'Croz & Maté 2004, Schlöder & D'Croz 2004). The nutrient-rich waters during upwelling furthermore promote the growth of phytoplankton and thereby reduce the light availability for benthic communities by increasing the turbidity of reef waters (D'Croz et al. 1991, D'Croz & Robertson 1997). Inorganic nutrients may also support the growth of benthic algae and may shift reef communities from coral to macroalgae dominance (Birkeland 1988, Bellwood et al. 2004, Fabricius 2005). Indeed, the green algae *Caulerpa sertularioides* is spreading aggressively along the Pacific coast of Costa Rica and threatens to overgrow coral reefs (Fernández & Cortés 2005). Cover and density of this algae increased during upwelling season, likely in response to high nutrient concentrations (Fernández-García et al. 2012). In Bahía Salinas, an area north of Bajo Rojo, the brown algae *Sargassum liebmanni* showed very high growth rates during the upwelling season in response to nutrient input (Cortés et al. 2014). On the other hand, higher concentrations of nutrients and plankton in the water can benefit coral nutrition by increasing zooxanthellae concentrations (Muscatine et al. 1989, Ferrier-Pagès et al. 2001, Roder et al. 2011) and food availability. Increased heterotrophic feeding by corals has the potential to compensate for reduced efficiency of symbionts, which often occurs in response to external stressors (Grottoli et al. 2006, Houlbrèque & Ferrier-Pagès 2009). Increased symbiont density and heterotrophic feeding may explain the high growth rates of corals in the Gulf of Papagayo during upwelling season (Jiménez & Cortés 2003).

We know of only few studies reporting similarly high pulses of organic matter and its implications in coral reefs. During a coral spawning event in the Great Barrier Reef, particulate organic nitrogen increased 3- to 11-fold to maximum concentrations of 300 µg PON L^{-1}, which resulted in a stimulation of oxygen consumption for one week and increased particulate organic matter and chlorophyll *a* concentrations in the reef water for two weeks (Wild et al. 2008). Nutrients released after coral spawning stimulated the autotrophic communities with 4.0- and 2.5-factor increases in pelagic and benthic production respectively for 4 - 5 days (Glud et al. 2008). The spawning studies showed that even these short term pulses of organic matter can influence the productivity of coral reefs and contribute substantially to reef nutrient budgets. In the Gulf of Papagayo, the effects of upwelling on chlorophyll *a* and organic matter lasted much longer and the accumulated input of nutrients and POM was

higher compared to these spawning studies. As a result of increased primary production, primary producer-derived DOC may affect activity and growth of microbial communities, which in turn play an important role in the remineralization of organic and inorganic matter (Ducklow et al. 1986) and transfer energy to higher trophic levels (Azam et al. 1993, Wild et al. 2004, 2005, 2009). The fact that DOC stayed elevated for several months after the initial nutrient pulses, indicates that the upwelling plays an important role in fueling the reef food web, particularly primary producers, at the study sites.

From the present study, upwelling can be considered the key driver that controls productivity and nutrient recycling in coral reefs at the northern Pacific coast of Costa Rica. Local coral communities have to adapt to a high variability in water parameters and elevated nutrient concentrations during upwelling. The cascading effects on chlorophyll *a* and organic matter concentrations in reef waters were higher and longer than reported for other areas, illustrating that the investigated Papagayo upwelling highly influences functions and services of local coral reefs.

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3 Seasonal changes in coral reef primary production at the upwelling-influenced Costa Rican Pacific coast

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Abstract

Photosynthetic primary production is a key ecosystem service provided by tropical coral reefs, but knowledge about the contribution of different organisms and the controlling environmental factors is scarce. Locations with occurrence of upwelling events can serve as natural laboratories to investigate these aspects in situ. This study evaluated the influence of seasonal upwelling on individual and reef-wide net (Pn) and gross primary production (Pg) by a range of dominant autotrophic benthic organisms (hard corals *Pocillopora* spp., crustose coralline algae (CCA), turf algae, and the macroalga *Caulerpa sertularioides*) in a coral reef of Pacific Costa Rica. Oxygen fluxes by these organisms were measured in a weekly to monthly resolution over one year (May 2013 - April 2014) via in situ chamber incubations. The effects of simultaneously measured environmental parameters (temperature, light, inorganic nutrient concentrations, dissolved and particulate organic matter concentrations) on Pn of the different taxa were tested via linear model fitting. Turf algae showed highest individual Pn and Pg rates per organism surface area (35 and 49 mmol O_2 m^{-2} h^{-1}), followed by *Pocillopora* spp. (16 and 25 mmol O_2 m^{-2} h^{-1}), CCA (9 and 15 mmol O_2 m^{-2} h^{-1}) and *C. sertularioides* (8 and 11 mmol O_2 m^{-2} h^{-1}). Pn rates of all algae taxa decreased by 12 - 15 % in the upwelling season (December - April) due to decreased temperature and light availability, while those of the corals increased by 35 % compared to non-upwelling season. On an ecosystem level, the coral on average contributed 60 % of total Pn and Pg per reef area (73 and 98 mmol O_2 m^{-2} h^{-1} respectively) due to its high benthic coverage, followed by turf algae (25 %). Individual O_2 fluxes and reef-wide primary production were relatively stable over the year of observation despite pronounced fluctuations of environmental parameters, indicating acclimatization of local primary producers to upwelling conditions.

3.1 Introduction

Photosynthetic benthic primary production represents a key ecosystem service provided by tropical coral reef systems. The conversion of light energy into chemical energy by photosynthesis creates the base of the food web in most terrestrial and aquatic ecosystems (Valiela 1995, Chapin et al. 2002). In coral reefs, primary production is tightly coupled with efficient utilization and regeneration of organic and inorganic nutrients, which allows an unusually high productivity in a nutrient poor environment (Muscatine & Porter 1977, Hallock & Schlager 1986). The main benthic primary producers in a coral reef are scleractinian corals with their endosymbiotic algae, crustose coralline algae, filamentous turf algae, fleshy macroalgae, and the microphytobenthos in the upper layer of reef sediments (Odum & Odum 1955, Hatcher 1988). The magnitude of primary production varies greatly within and among coral reefs due to spatial differences in benthic community composition as well as spatial and temporal changes in environmental conditions (Hatcher 1990, Gattuso et al. 1998). Primary production is determined by three main factors: light intensity (Muscatine et al. 1984, Hatcher 1990), seawater temperature (Hatcher 1990, Wild et al. 2011), and nutrient availability (Delgado & Lapointe 1994, Larned 1998, Schaffelke 1999). Coral reefs are facing changes in these environmental parameters, but potential implications for reef primary productivity are rarely known. Physiological studies on coral reefs that are naturally exposed to a high variability in environmental conditions can provide essential information in this context.

Locations with upwelling events can be used as natural laboratories for in situ studies, as coral reefs experience large variations in water chemistry when sub-thermocline water enters the surface layer. The upwelling usually decreases water temperature and pH, while concentrations of inorganic nutrients and dissolved inorganic carbon (DIC) increase (Pennington et al. 2006, Fassbender et al. 2011, Rixen et al. 2012). Upwelling nutrients can increase primary production and phytoplankton concentrations in the water column (D'Croz & O'Dea 2007), which in turn may decrease light availability to the benthos (Kirk 1994, Van Duin et al. 2001). Upwelling may therefore contrarily affect benthic primary production: higher inorganic nutrient availability may increase photosynthetic activity of benthic algae and coral symbionts, whereas lower water temperature and light levels may decrease benthic photosynthesis. It is likely that different primary producers react differently to upwelling conditions. Macroalgal density and production is highly dependent on light and inorganic nutrient availability (Delgado & Lapointe 1994, van Tussenbroek 2011). Turf algae are also very important primary producers on coral reefs and may benefit largely from nutrient pulses due to their rapid nutrient uptake rates (Carpenter 1990). In contrast, corals are usually adapted to oligotrophic environments (Hallock & Schlager 1986), although symbiont densities may increase with increased nutrient concentrations (Szmant

2002, Roder et al. 2011). Most studies found that corals are at disadvantage compared to algae when nutrient levels are high (Jompa & McCook 2002, Haas et al. 2009, Vermeij et al. 2010). This may be particularly the case for nutrient pulse events such as upwelling, from which fast growing species could benefit the most. Cold water stress may have further negative impacts on coral photosynthetic efficiency and pigment concentration (Saxby et al. 2003) and can even cause cold water bleaching (Glynn & D'Croz 1990, Jiménez 2001, Saxby et al. 2003).

While most former studies on benthic coral reef primary production focused on spatial comparisons of primary productivity, we were interested in the temporal variability in primary production in response to upwelling. Introduction of subthermocline water to shallow reefs increased primary productivity in the Colombian Caribbean (Eidens et al. 2012, 2014) and the Andaman Sea (Jantzen et al. 2013). The temporal resolution of these studies was low, and the relative importance of driving environmental parameters was not evaluated. With our study we aimed to investigate if seasonal upwelling at the Pacific coast of Costa Rica influences in situ primary production and respiration rates in eastern tropical Pacific coral reefs and which environmental parameters drive these changes in different benthic primary producers. Main objectives were to (1) quantify individual primary production and respiration rates for all dominant primary producers in a high temporal resolution over one year, (2) calculate total net and gross primary production of primary producers in the investigated reef and the relative contribution of each organism group, and (3) analyze the influence of simultaneously measured environmental parameters on productivity parameters of each organism group.

3.2 Material and Methods

3.2.1 Study site and seasonality

The study was carried out from May 2013 to April 2014 in a shallow fringing reef at Matapalo in the Gulf of Papagayo, Costa Rica, which is influenced by seasonal upwelling. Matapalo reef extends about 1 km along the northern coast of the Nicoya Peninsula in the Bay Matapalo (Fig. 3.1). The reef structure is built by the branching coral *Pocillopora* spp. with alternating patches of dead and living carbonate structure in 3 - 8 m water depth. An area of around 600 m^2 with relatively high live coral cover compared to the surrounding area was visited almost weekly to conduct water samplings and incubation experiments.

The Papagayo region is subjected to strong seasonality caused by the intensification of trade winds during the northern hemisphere winter (McCreary et al. 1989, Amador et al. 2006). These northeasterly wind jets displace superficial water away from the coast and cause upwelling of sub-thermocline cold and nutrient-rich waters to the surface (Fiedler

& Talley 2006, Pennington et al. 2006). Seasonal upwelling decreases mean seawater temperatures from around 28 °C down to 23 °C between December and April (Jiménez 2001, Alfaro et al. 2012), which is accompanied by drops in pH and oxygen concentration (Rixen et al. 2012). Nutrient concentrations of up to 15.6 µmol L^{-1} nitrate and 1.5 µmol L^{-1} phosphate were measured in 15 m water depth in the Gulf of Papagayo during upwelling months (Fernández-García et al. 2012).

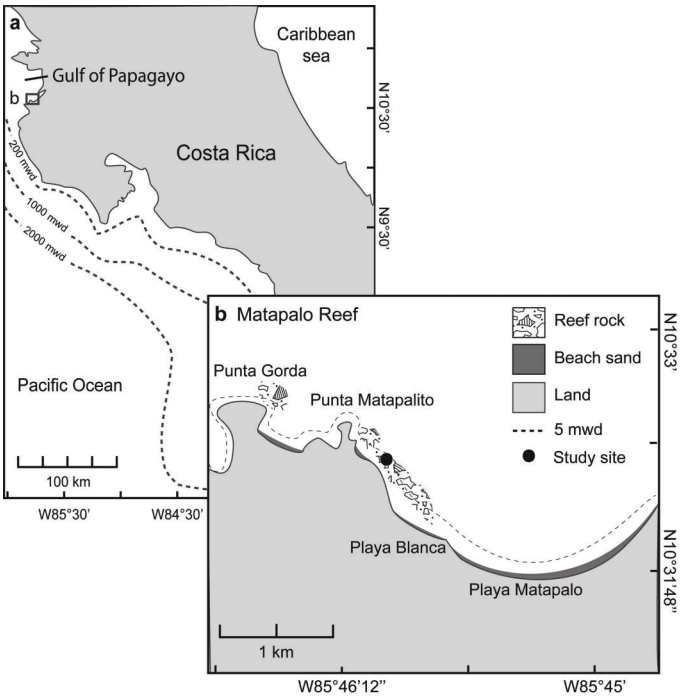

Figure 3.1: Study site. (a) Location of Matapalo Reef at the northern Pacific coast of Costa Rica. (b) Indication of study site at 5 m water depth where incubations and benthic surveys took place (10°32'21"N, 85°45'59"W).

3.2.2 Environmental parameters

A range of environmental parameters were measured weekly at the study site to investigate the influence of upwelling on primary production in the reef. Water temperature was determined parallel to oxygen measurements at the time of incubations (see section 3.2.4) using an optical dissolved oxygen (DO) sensor (FDO® 925, WTW). Light conditions during incubations were measured using a self-contained PAR logger with a planar cosine-corrected sensor (Odyssey Integrating PAR sensor, Dataflow Systems PTY Limited). The logger was placed among the incubation chambers and recorded integrated light availability over 2 min time intervals. Because a 1-point calibration in air does not produce reliable estimates of irradiance under water, the produced millivolt signal was calibrated to µmol photons

m^{-2} s^{-1} using an exponential fit according to Long et al. (2012):
PAR = -4924.7 × $e^{(-ODY/20992.9)}$ + 4929.0
where ODY is the raw output data (mV) of the Odyssey data logger multiplied with 7.5 to obtain the same integration time as in the Long et al. (2012) study (15 min). A mean value over each incubation period was calculated for further statistical analyses.

Daily temperature range (maximum − minimum temperature) was calculated from continuous temperature measurements (HOBO® Pendant Temperature Data loggers) as a measure for upwelling intensity for each incubation day (Jantzen et al. 2013). Water for the determination of inorganic nutrient concentrations (phosphate PO_4^{3-}, nitrate NO_3^- and ammonia NH_4^+) and dissolved organic carbon (DOC) was sampled in triplicate from directly above the reef substrate. Water for chlorophyll *a* (chl *a*) and particulate organic carbon (POC) as well as nitrogen (PON) was sampled in triplicate from around 20 cm below the sea surface over the reef. Measurements and results of abiotic parameters are described in detail in Stuhldreier et al. (in review). Missing values for DOC and POC/PON at the beginning of the study period (see Fig. 3.4) resulted in smaller sample sizes for some of the fitted models (see section 3.2.5).

3.2.3 Benthic community and study organisms

Cover of benthic organisms and substrate on Matapalo reef was quantified monthly at 5 m water depth along five permanent transects of 10 m length (marked with iron poles every 5 m), using the chain method (Rogers et al. 1994). An iron chain of 10 m length with 532 links was placed directly on the reef structure, following its contours, and thereby taking into account the structural complexity of the reef. Benthic cover was determined under each link (live coral and macroalgae to species level, dead coral, crustose coralline algae (CCA), turf algae, cyanobacteria, sand) and the number of links was later converted to relative seafloor cover.

The dominant primary producers in the reef in 5 m water depth were identified as the scleractinian corals *Pocillopora* spp. (35.4 ± 1.3 % relative cover), turf algae (28.8 ± 1.4 %), crustose coralline algae (29.2 ± 1.6 %) and the green algae *Caulerpa sertularioides* (4.0 ± 0.7 %; mean values ± SE over the study period). This selection of organisms together accounted for 97 % of the reef coverage and was therefore chosen to represent all primary producers in the reef. Four specimen of each organism group were sampled for incubation experiments from the reef or the surrounding sand flat using SCUBA on each of the 33 incubation days. Small, loose live coral fragments and dead coral fragments overgrown with CCA could be found easily on the sand area bordering the reef. Therefore it was not necessary to break coral colonies or reef structure overgrown with CCA, which would have resulted in damaged coral or algal tissue. Care was taken to use coral and CCA fragments of approximately the

same size and a simple shape to ensure consistent results. Dense turf algae conglomerates were removed from dead coral rock, and *C. sertularioides* was collected as pieces of stolons with associated fronds.

For surface area quantification of incubated organisms, the average diameter and height of coral fragments, CCA fragments and turf algae conglomerates were measured with a caliper, and surface areas were calculated for all three taxa with the best fitting geometric shape (cylinder; Naumann et al., 2009). In case of coral fragments we additionally multiplied the result with the proposed approximation factor for *Pocillopora* spp. (0.94) according to Naumann et al. (2009). Surface area of *C. sertularioides* was calculated by average length × width of algal fronds, multiplied by the factor 2 to account for both sides, and multiplied by the number of fronds.

3.2.4 Incubation experiments

Four specimen of each organism group were incubated immediately after collection in direct proximity to the reef inside 500 mL gas-tight glass chambers with surrounding seawater as medium to quantify individual net primary production (Pn) under in situ water and light conditions. Incubations started between 10:30 and 11:30 or 13:30 and 14:30 to ensure high in situ light availability, while avoiding peak irradiances between 12:00 and 13:00. Time of incubation was not correlated to primary production rates ($F(28,103) = 0.676$, $p = 0.882$), indicating that different times of incubations did not confound effects of other parameters. Three incubation chambers containing only seawater served as controls for incubations, while one chamber was closed with the others and immediately brought to the surface to measure the start DO concentration and temperature using an optical DO sensor (FDO®925, WTW). After around 70 min of incubation, all glass chambers were transported to the surface, and the concentration of DO was measured in the incubation medium of each chamber after gently stirring for 5 - 10 seconds until the signal stabilized to ensure homogeneous DO distribution.

Every month, the incubated specimen and four seawater controls were subsequently incubated for around 70 min in fresh surface seawater in a dark cooler on the boat to obtain individual respiration rates (R). All incubations were conducted under no-flow conditions, which allowed for comparison with previous chamber incubation studies (Naumann et al. 2013, Jantzen et al. 2013, Eidens et al. 2014). As water flow may enhance O_2 fluxes (Mass et al. 2010), the results of the field incubations are conservative estimates of in situ O_2 fluxes and should be interpreted accordingly.

3.2.5 Data analyses and statistics

Organism-specific primary production

Pn and R for each incubated specimen were derived from DO concentration differences in the incubation medium calculated by subtracting start from end concentrations. These results were corrected for DO concentration differences measured in seawater controls and normalized to specimen surface area and incubation period. Gross primary production (Pg) was calculated by adding R to Pn for each incubated specimen. Rates from specimen of the same taxa and incubation day were averaged resulting in almost weekly individual Pn (n = 33) and monthly R and Pg rates (n = 12) for each incubated taxa, given in mmol O_2 m^{-2} organism surface area h^{-1}. The general influence of upwelling on overall and organism-specific Pn, Pg and R rates was determined using one-way Analyses of Variance (ANOVA) comparing values obtained between May and November 2013 (non-upwelling season) against values between December 2013 and April 2014 (upwelling season) using the software R 3.1.1 (R Core Team 2014).

Reef-wide primary production

The contribution of each individual organism group to reef-wide Pn and Pg for each month was estimated as follows (Eidens et al. 2014): $c_i = P_i \times b_i \times s_i$
Taxa specific c_i was thereby calculated from the benthic group's individual production rate (P_i), their respective 2D benthic cover in the reef (b_i) and group specific mean 2D to 3D conversion factors (s_i). The 2D to 3D conversion factors were obtained from the literature and valued 6.8 for *Pocillopora* spp. (Alcala & Vogt 1997), 2.1 for CCA (Eidens et al. 2014), 1.5 for turf algae (Jantzen et al. 2013) and 14 for *C. sertularioides* (Naumann et al. 2013). Eidens et al. (2014) additionally included a rugosity factor in this calculation, which we accounted for already by using the chain method for benthic community assessment (see section 3.2.3). Total reef-wide benthic net (total Pn) and gross primary production (total Pg) were calculated by summing up the contributions of the individual taxa (c_i) and are expressed as mmol O_2 m^{-2} reef area h^{-1}. Total reef-wide Pn should not be confused with net ecosystem production, which would include respiration of heterotrophic organisms. Differences between non-upwelling and upwelling season were determined using one-way Analyses of Variance (ANOVA) in the software R 3.1.1 (R Core Team 2014). Hourly total Pn and Pg rates were not extrapolated to daily rates for the seasonal comparison of total reef primary production, as we do not consider one hour incubations around midday to be representative for a 12 h light and 12 h dark cycle. However, comparisons with other reef budget studies using daily estimates are discussed in section 3.4.3.

Correlation of primary production and environmental parameters

We used model selection in the software R 3.1.1 (R Core Team 2014) to determine which combination of the ten measured environmental parameters (incubation temperature, daily temperature range, light, PO_4^{3-}, NO_3^-, NH_4^+, DOC, chl *a*, PON and POC) best predicted the measured overall and organism-specific production rates. Parameters were z-transformed and tested for multicollinearity using scatterplot matrices and correlation coefficients based on restricted maximum likelihood estimates. Removing collinearity is important because explanatory parameters may mask each others' influences on the response parameter and reduce the explanatory power of the model. Collinear parameters were removed resulting in 6 explanatory variables with pairwise correlation coefficients ≤ 0.6: temperature (*incubation temperature*, daily temperature range), light (only for Pn and Pg), nutrients (NH_4^+, PO_4^{3-}, NO_3^-), DOC and particulate organic matter POM (*POC*, PON, chl *a*). The factor which represents their respective group in statistical analyses is indicated in italics. Linear models were fit to log(x+1)-transformed Pn, Pg and R data including all six explanatory variables. Minimum adequate model selection was then performed using Akaike's Information Criterion (AIC) and adjusted R^2 (indicating the amount of variance in the data explained by the respective model) before being tested for significant influences of remaining parameters using multiple regression with adjusted sum of squares (function 'Anova' in package 'car'). The models for overall Pn, Pg and R data included taxa and its interactions with the environmental parameters as explanatory variables, while models for Pn rates of single taxa only tested the influence of environmental parameters. We did not model the influence of environmental parameters on Pg and R data of individual taxa, because assumptions of normality were violated with the sample sizes of n = 12.

3.3 Results

3.3.1 Organism-specific primary production

Of all investigated functional groups, individual primary production and respiration rates were highest for turf algae, followed by *Pocillopora* spp., CCA and *C. sertularioides* (Table 3.1). Pn and Pg rates significantly differed between taxa ($F(3,128) = 62.469$, $p < 0.0001$ and $F(3,44) = 44.506$, $p < 0.0001$ respectively) except comparing CCA and *C. sertularioides*. R rates significantly differed between taxa ($F(3,44) = 20.464$, $p < 0.0001$) except comparing *Pocillopora* spp. and turf algae. Pn rates of the coral *Pocillopora* spp. significantly increased by 35 % in upwelling compared to non-upwelling season ($F(1,31) = 4.693$, $p = 0.0381$), but decreased 12 - 15 % for all algae groups (Fig. 3.2). Pg rates showed the same pattern, but none of the differences was significant.

Table 3.1: Mean primary production and respiration rates of the dominant benthic primary producers.

	Pn	Pg	R	Pn:R
	(mmol O_2 m^{-2} organism surface area h^{-1})			
Turf algae	35.0 ± 2.9 (33)	49.1 ± 4.4 (12)	8.2 ± 0.8 (12)	5.6 ± 1.2 (12)
Pocillopora spp.	15.5 ± 1.1 (33)	25.2 ± 2.2 (12)	7.2 ± 0.7 (12)	2.6 ± 0.2 (12)
CCA	8.8 ± 0.6 (33)	14.5 ± 0.9 (12)	4.4 ± 0.7 (12)	3.2 ± 0.5 (12)
C. sertularioides	7.8 ± 0.5 (33)	11.1 ± 1.1 (12)	1.8 ± 0.2 (12)	6.1 ± 0.7 (12)

Values for Pn, Pg and R as well as Pn:R were calculated from taxa specific values over all incubation occasions and are given as mean ± SE (number of replicates). Abbreviations: Pn = net primary production, Pg = gross primary production, R = respiration.

Respiration increased in upwelling compared to non-upwelling season in the taxa *Pocillopora* spp. and CCA, although these differences were not significant. As a result, R rates of *Pocillopora* spp. did exceed those of turf algae during upwelling season (Fig. 3.2). Individual respiration rates of all taxa were much smaller than respective net photosynthetic rates, resulting in mean Pn:R ratios of around 3 (*Pocillopora* spp. and CCA) to 6 (turf algae and *C. sertularioides*) (Table 3.1). While the ratio was constant over the year of observation for *Pocillopora* spp., ratios of CCA, turf algae and *C. sertularioides* decreased in upwelling (2.0, 3.8 and 5.1 respectively) compared to non-upwelling season (4.0, 6.9 and 6.7 respectively). The difference was significant only for CCA ($F(1,10) = 5.989$, $p = 0.034$). All statistical results can be found in Supplementary Table S3.1.

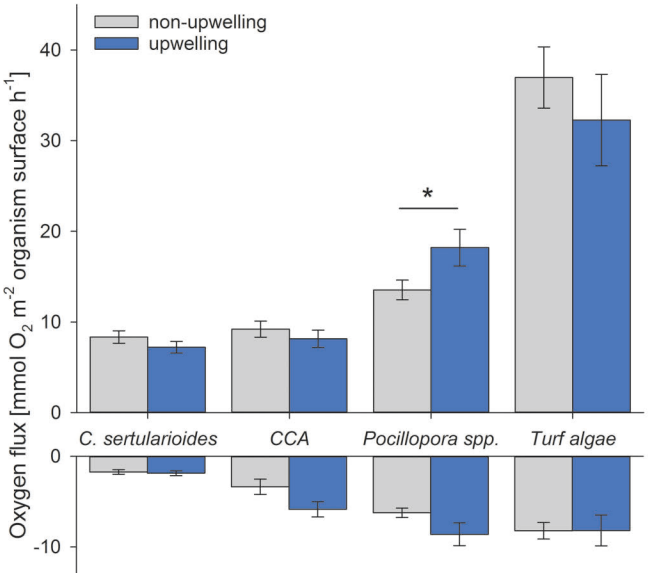

Figure 3.2: Organism-specific oxygen fluxes. Net primary production (positive) and respiration rates (negative) of the dominant primary producers (in mmol O_2 flux normalized to organism surface area) comparing non-upwelling (May - Nov) and upwelling season (Dec - Apr).

3.3.2 Reef-wide primary production

The combination of taxa-specific production and respiration rates with relative benthic coverage and 2D-3D conversion factors enabled us to calculate total net and gross primary production of all primary producers in the investigated reef in a monthly resolution (Fig. 3.3a). Reef-wide total Pn and Pg were higher in upwelling compared to non-upwelling season, but differences were non-significant ($F(1,10) = 0.592$, $p = 0.4594$ and $F(1,10) = 1.960$, $p = 0.1918$ respectively; Fig. 3.3b). The relative contribution of primary producer groups to total Pg was highest for *Pocillopora* spp. over the whole year of observation and significantly increased from 55 ± 2 % in non-upwelling season to 70 ± 2 % in upwelling season ($F(1,10) = 32.5$, $p = 0.0002$, Fig. 3.3d), as individual production rates and benthic cover increased. The contribution of turf algae to total Pg significantly decreased from 29 ± 2 % in non-upwelling to 15 ± 2 % in upwelling season ($F(1,10) = 32.3$, $p = 0.0002$), while relative contributions of CCA and *C. sertularioides* did not differ significantly between seasons (Fig. 3.3d).

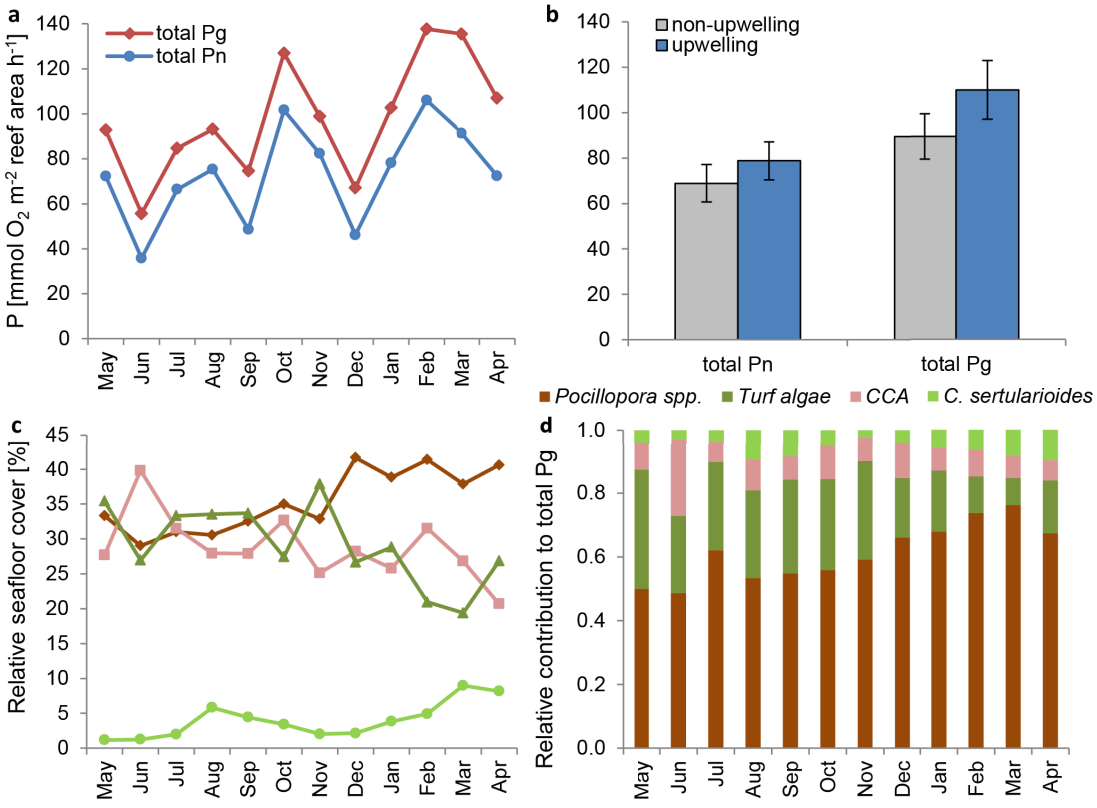

Figure 3.3: Reef-wide primary production. (a) Total reef-wide net (total Pn) and gross primary production (total Pg) from May 2013 to April 2014 in a monthly temporal resolution and (b) comparing non-upwelling (May to November 2013) and upwelling season (December 2013 to April 2014). (c) Relative seafloor cover of dominant primary producers over the year of observation and (d) their relative contribution to monthly total Pg (calculated from (a) and (c)).

3.3.3 Correlation of primary production to environmental parameters

Overall and individual oxygen production rates showed a considerable variability over the study period, potentially related to differences in water parameters (Fig. 3.4).

Overall primary production and respiration

The variability in overall Pn data was best explained by a model including the explanatory variables taxa, temperature, light, nutrients, DOC and the interactions between taxa and the parameters temperature and DOC. These variables together explained 71 % of the variability in the data (adjR^2 = 0.71) and all parameters except DOC and the two interaction terms significantly influenced overall production rates. The variability in Pg data was best explained by the variables taxa, light, DOC, POC and the interaction between taxa and POC (adjR^2 = 0.91), from which all except POC were significant. The variability in overall R data was best explained by the variables taxa, temperature, POC and the interaction term of taxa and temperature (adjR^2 = 0.77) from which taxa and temperature significantly influenced overall respiration rates. All statistical results can be found in Supplementary Table S3.2.

Organism-specific net primary production

Production rates of *Pocillopora* spp. were influenced by the variables light, nutrients and DOC (adjR^2 = 0.38) and significantly increased with increasing light ($F(1,20) = 6.978$, $p = 0.0157$) and DOC levels ($F(1,20) = 6.766$, $p = 0.0171$). For production rates of CCA, no combination of the measured parameters could explain the variability in the Pn data. Production rates of turf algae were influenced by the variables temperature, light, nutrients and DOC (adjR^2 = 0.33) and significantly increased with increasing temperature ($F(1,19) = 7.322$, $p = 0.0140$), light ($F(1,19) = 6.971$, $p = 0.0161$) and nutrients ($F(1,19) = 4.932$, $p = 0.0387$). Production rates of *C. sertularioides* were influenced by temperature, light and nutrients (adjR^2 = 0.43) and significantly increased with increasing temperature ($F(1,28) = 13.684$, $p = 0.0009$), light ($F(1,28) = 6.838$, $p = 0.0142$) and nutrients ($F(1,19) = 6.953$, $p = 0.0135$). See Supplementary Table S3.2 for further details of statistical tests.

3.4 Discussion

This study represents one of few field investigations comparing primary production rates of different coral reef primary producers (Wanders 1976, Eidens et al. 2012, 2014, Naumann et al. 2013). To our knowledge, it is the first study to correlate in situ organism-specific metabolic rates to seasonal variations in environmental conditions. Our findings characterize the investigated reef as a net autotrophic benthic environment dominated by the scler-

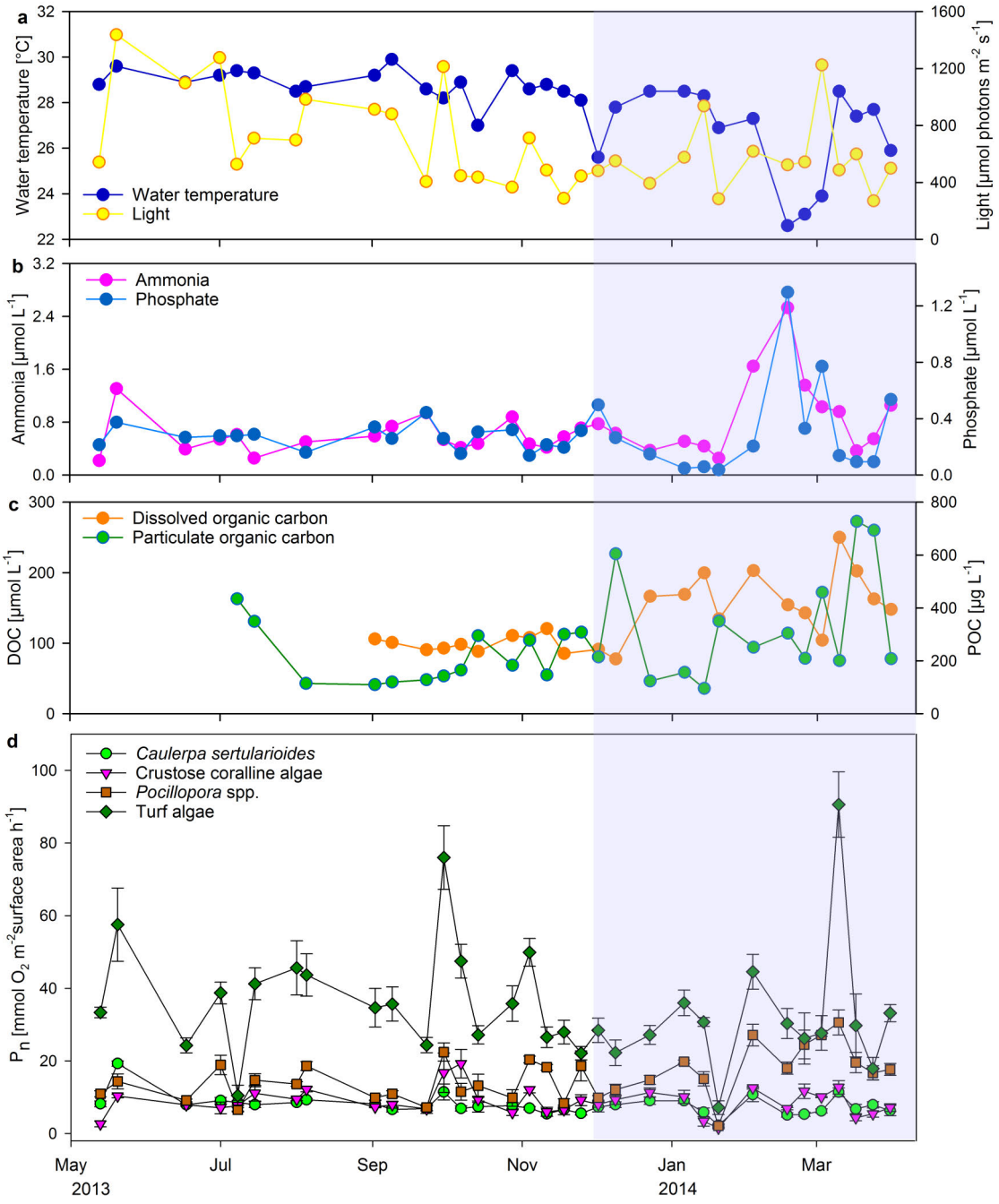

Figure 3.4: Seasonal changes in water parameters and individual net primary production. (a) Water temperature and light availability in 5 m water depth, (b) inorganic nutrient concentrations of ammonia and phosphate, (c) dissolved and particulate organic matter and (d) net primary production (Pn) rates of main primary producers in the reef. Given values are means (± SE for Pn).

actinian coral *Pocillopora* spp. and turf algae, which due to their high production rates are also the major contributors to photosynthetic primary production in the reef. In contrast to prior hypotheses, increased photosynthetic rates of *Pocillopora* spp. in the upwelling season suggest a competitive advantage of corals over algae under upwelling conditions.

3.4.1 Organism-specific primary production

Individual production and respiration rates were in the range of previous reference studies (Wanders 1976, Hatcher 1988, Chisholm 2003, Eidens et al. 2014). In the present study, individual production rates of turf algae were 2 - 4-fold higher compared to other investigated primary producers. In contrast, most studies observed individual rates of corals to be equal or even higher than turf algae production (Wanders 1976, Hatcher 1990, Eidens et al. 2014). As turf algae are diverse conglomerates of different filamentous algae and cyanobacteria, it is not surprising that rates differ greatly between studies. We used very dense conglomerates of turf algae communities which may explain the relatively high production rates.

The effects of upwelling on overall and taxa-specific primary production in the present study were relatively low and only significant for Pn rates of *Pocillopora* spp. This lack of seasonality may be due to upwelling related changes in various abiotic factors that compensate for each other. While low water temperatures and light levels usually decrease the photosynthetic performance of primary producers in coral reefs (Gladfelter 1985, Hatcher 1988), high nutrient concentrations may increase the productivity of mainly nutrient-limited turf and macroalgae (Szmant 1997, Carpenter & Williams 2007) and the symbiont density and chlorophyll *a* content in corals (Szmant 2002). During upwelling, net and gross production rates of *Pocillopora* spp. increased, while that of all algae taxa decreased. Eidens et al. (2014) found an opposite pattern for the Caribbean with decreased productivity rates of corals and increased rates for turf and CCA in the upwelling season. In general, most studies showed that corals are at disadvantage compared to algae when nutrient levels are high (Jompa & McCook 2002, Haas et al. 2009, Vermeij et al. 2010). The competitive advantage of corals over algae in the present study may therefore be caused by other upwelling related factors as discussed in section 3.4.2.

Respiration rates of *Pocillopora* spp. and CCA increased during upwelling. While this effect was balanced by higher production rates in the coral, the Pn:R ratio of CCA decreased. Ratios of turf algae and *C. sertularioides* also decreased in upwelling season due to decreased Pn rates. The decreasing Pn:R ratios of CCA, turf algae and *C. sertularioides* during upwelling indicate that these organisms may have been subjected to temperature- (Beyers 1962) or light-stress (Copeland 1965). On the other hand, the coral *Pocillopora* spp. at the study site seemed to be able to acclimatize to pronounced changes in environmental parameters, and was the only primary producer of the present study that benefited from up-

welling conditions in terms of productivity. The differences in susceptibility to upwelling indicate that different environmental factors may differently influence individual primary producers.

3.4.2 Environmental factors driving primary production

Depending on the sensitivity of different organisms to certain environmental factors, upwelling can be beneficial for some primary producers, while decreasing the performance of others. Photosynthetic performance of algal turfs increased 2.0-fold in the Caribbean during the upwelling season (Eidens et al. 2014) and 1.4-fold in the Andaman Sea on island sides exposed to large amplitude internal waves (Jantzen et al. 2013), which the authors related to increased nutrient concentrations and water currents. Although Pn rates of turf algae and *C. sertularioides* in our study were likewise positively correlated to nutrient concentrations, net and gross primary production of these algal taxa was lower in upwelling season when nutrient concentrations were highest. Our results and previous studies showed productivity of turf algae and macroalgae strongly and positively correlated with light availability (Gladfelter 1985, Adey & Goertemiller 1987), with a lack of photoinhibition in turf algae (Klumpp & McKinnon 1992). The decrease in algal Pg and Pn from non-upwelling to upwelling season in the present study may therefore be accounted to overall lower light and temperature levels in the upwelling season ($F(1,130) = 9.136$, $p = 0.0030$ and $F(1,130) = 85.369$, $p < 0.0001$ respectively). Light availability and temperature therefore seem to be of higher importance in controlling turf algae and fleshy macroalgae primary production at the study site than nutrients.

Pn rates of *Pocillopora* spp. were also positively correlated to light availability, but the increased productivity of corals in upwelling season suggests that other upwelling related parameters compensated for the negative effects of low water temperature and light levels. In our models, DOC came up as the main controlling factor for coral net primary production. It is likely that the elevated DOC concentrations are a result of increased productivity rates and excess release of organic matter during upwelling instead of driving primary production. All photosynthesizing benthic organisms release part of their fixed carbon into the water column as DOC, but benthic algae can release more DOC than corals (Wild et al. 2010, Haas et al. 2011, 2013). Macroalgal labile DOC fuels the growth of heterotrophic microbes associated with corals and algae (Smith et al. 2006, Nelson et al. 2013, Haas et al. 2013), which may negatively affect corals by increasing the dominance of pathogenic bacteria (Kline et al. 2006, Dinsdale et al. 2008, Nelson et al. 2013), or by causing local hypoxia leading to coral tissue mortality (Barott et al. 2009, Wild et al. 2010, Haas et al. 2011). In contrast to these findings, we found DOC concentrations positively correlated with *Pocillopora* spp. primary production. As *Pocillopora* spp. was the main contributor to reef-wide

benthic net and gross photosynthesis, it is possible that they produced most of the available DOC in the reef water. If the system is well flushed, and the DOC is refractory, microbes will not degrade the compounds on site, which may explain the absence of negative effects on the study site. Factors which were not considered in this study may have benefited coral primary production during upwelling, such as increased food availability for heterotrophic feeding. Increased heterotrophy may enhance rates of photosynthesis by increasing symbiont density and chl *a* content in the coral (Dubinsky et al. 1990, Titlyanov et al. 2000, Houlbrèque et al. 2003). By increasing symbiont density and chl *a* content, both nutrients and heterotrophic feeding can thereby enhance acclimation to reduced light conditions (Anthony & Fabricius 2000, Titlyanov et al. 2000) and low water temperatures (Wellington & Glynn 1983, Manzello 2010). The ability to feed heterotrophically may therefore offset the negative impacts of reduced light and temperature during upwelling and explain the competitive advantage of corals over benthic algae in terms of primary production during the upwelling season.

The variability in production rates of CCA could not be explained by the combination of measured parameters. Additional factors are likely important for metabolic processes of these organisms, e.g. wave energy or herbivory. Taking into account such factors may also increase the explanatory power of the models for other taxa and is therefore suggested for future analyses.

3.4.3 Reef-wide primary production

In the studied reef, *Pocillopora* spp. contributed most to total reef-wide Pg in both non-upwelling and upwelling season, due to high individual primary production rates, a high benthic coverage, and the corals' structural complexity. Dominant contribution of corals to reef-wide Pg was also observed in a Caribbean upwelling system (Eidens et al. 2014). In contrast, turf algae were the main contributors to reef primary production in areas exposed to large amplitude internal waves (Jantzen et al. 2013) or rain-induced nutrient plumes (den Haan 2015) due to the algal's high individual photosynthetic rates in combination with high relative substrate cover.

It has been recognized that daily reef primary production varies dramatically among reefs, sometimes in 1 - 2 orders of magnitude (Adey & Steneck 1985, Hatcher 1990). Besides large variations in environmental settings, this may partly be due to different measuring techniques and calculation methods, especially when extrapolating measured values to daily production rates. We nevertheless want to provide a comparison with reef-wide production rates from different locations as, until now, no primary production rates have been published for the eastern tropical Pacific. If we assume a 12:12 h day/night cycle, as typical for the tropics, and extrapolate our hourly values to daily estimates of reef-wide Pg

(total Pg h^{-1} x 12 h sunlight) and Pn (total Pn h^{-1} x 12 h sunlight - total R h^{-1} x 12 h night) we end up with magnitudes of total reef production in the upper range of most comparable studies and considerably higher than some (Table 3.2). Because incubations took place in relatively high light intensities around midday, realistic daily values are likely lower than calculated by simple extrapolation to 12 h, but still hint to a highly productive reef system in the upwelling region of Papagayo. Differences to the studies of Hatcher (1990) and Eidens et al. (2012, 2014) could be due to water depth effects, as those studies were conducted at around 10 m water depth where the light availability and therefore primary production is lower. Values from a reef in 6 m depth are very similar to our estimates (Adey & Steneck 1985). In general, back and fore reef communities differ greatly in production rates, with much higher production rates for shallow back reefs (Adey & Steneck 1985, Hatcher 1988). The range of total daily Pg and Pn data in our study was high compared to studies by Hatcher (1990) and Eidens et al. (2012, 2014), which could be attributed to their much smaller sample size (n = 4 compared to n = 12).

It has been suggested that Caribbean reefs are more productive than Pacific reefs (Adey & Steneck 1985, Hatcher 1990). The present study does not confirm this assumption; in fact, reef production was higher than in several Caribbean coral reefs. Upwelling regions usually support very productive ecosystems (Birkeland 1988) what is likely the main reason for the high productivity observed at the study site. This assumption is also supported by higher total Pn and Pg during upwelling, although the differences were not significant. Another reason may be the high structural complexity of the dominating branching coral *Pocillopora* spp., as the increased light capturing capabilities of branching corals facilitate higher production rates compared to massive or plating growth forms (Smith 1981).

Despite the relatively high variability in total Pn and Pg rates over time, differences in production rates were not seasonal (no significant differences in non-upwelling and upwelling season). In contrast, prior studies found approximately two-fold differences in benthic pri-

Table 3.2: Daily total reef primary production in various coral reef ecosystems.

Reference	total Pg (mmol O_2 m^{-2} reef area d^{-1})	total Pn	Reef type and region
Present study	667 - 1652	191 - 916	Reef 5 m depth, Costa Rica, eastern Pacific
Wanders (1976)	1294	531	Reef 0.5-3 m depth, Curaçao, Caribbean
Kinsey (1985)	333 - 1665		Reef flat, various locations
Adey&Steneck (1985)	626 - 1275	225 - 938	Fore reef 6 m depth, St. Croix, Caribbean
Hatcher (1988)	167 - 583	-83 - 425	Fore reef, various locations
Eidens et al. (2012)	250 - 483	125 - 272	Reef 10 m depth, Colombia, Caribbean
Eidens et al. (2014)	250 - 305	103 - 169	Reef 10 m depth, Colombia, Caribbean

Minimum and maximum values of total reef-wide gross (total Pg) and net primary production (total Pn) for different reef locations. If necessary, original units were converted to O_2 estimates assuming a C:O_2 metabolic quotient equal to one.

mary production between seasons, with higher productivity in summer (Kinsey 1977, 1985, Smith 1981) or during upwelling (Eidens et al. 2012). The variability in total Pn and Pg rates over the year in the present study was apparently more strongly influenced by differences in conditions at the day of incubations than by differences between seasons. The fact that daily variations are able to override upwelling influences suggests acclimatization mitigated responses of the benthic community to seasonal variations in water parameters.

3.4.4 Outlook

The observed similarity in individual productivity rates between non-upwelling and upwelling months suggest that eastern tropical Pacific primary producers are adapted to pronounced seasonal variations in light availability, water temperature, and nutrient availability. In contrast to benthic algae, the coral *Pocillopora* spp. seems to benefit from upwelling conditions if temperatures do not decrease below detrimental limits of <15 °C, which caused bleaching and mortality in local corals (Glynn et al. 1983, Jiménez 2001).

The constantly high benthic productivity over the year suggests a generally high resilience of local benthic communities against present and maybe also future environmental fluctuations. It is likely that interannual variations affect the productivity of eastern tropical Pacific coral reefs as it was shown for the Caribbean (Eidens et al. 2014), which could be investigated by repeated incubation experiments over several seasons and years. It would furthermore be interesting to investigate if reef accretion exceeds erosion of the reef substrate over the entire year, and how multiannual stressors such as El Niño events or harmful algae blooms affect primary production in the reef. Only reefs with stable net growth despite strong fluctuations in environmental parameters may be less susceptible to future environmental changes.

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Supplementary Tables

Supplementary Table S3.1: Statistical results of ANOVAs and post hoc tests comparing oxygen fluxes between organisms and seasons

1. Differences in oxygen fluxes comparing organisms

Response parameter: Pn	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
organism	3	15721.0	5240.3	62.469	2.20E-16	***
Residuals	128	10737.0	83.9			
Tukey HSD		diff	lwr	upr	p adj	
CCA - *C. sertularioides*		0.900	-4.969	6.769	0.9784	ns
Pocillopora spp. - *C. sertularioides*		7.651	1.782	13.521	0.0050	**
Turf algae - *C. sertularioides*		27.110	21.241	32.980	0.0000	***
Pocillopora spp. - CCA		6.751	0.882	12.621	0.0172	*
Turf algae - CCA		26.211	20.341	32.080	0.0000	***
Turf algae - *Pocillopora* spp.		19.459	13.590	25.329	0.0000	***
Response parameter: Pg	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
organism	3	10607.0	3535.7	44.506	2.21E-13	***
Residuals	44	3495.5	79.4			
Tukey HSD		diff	lwr	upr	p adj	
CCA - *C. sertularioides*		3.422	-6.293	13.138	0.7833	ns
Pocillopora spp. - *C. sertularioides*		14.076	4.360	23.791	0.0020	**
Turf algae - *C. sertularioides*		38.002	28.286	47.717	0.0000	***
Pocillopora spp. - CCA		10.653	0.938	20.369	0.0267	*
Turf algae - CCA		34.579	24.864	44.295	0.0000	***
Turf algae - *Pocillopora* spp.		23.926	14.211	33.642	0.0000	***
Response parameter: R	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
organism	3	304.1	101.4	20.464	1.88E-08	***
Residuals	44	218.0	5.0			
Tukey HSD		diff	lwr	upr	p adj	
CCA - *C. sertularioides*		-2.624	-5.050	-0.198	0.0295	*
Pocillopora spp. - *C. sertularioides*		-5.453	-7.879	-3.027	0.0000	***
Turf algae - *C. sertularioides*		-6.428	-8.854	-4.002	0.0000	***
Pocillopora spp. - CCA		-2.829	-5.255	-0.403	0.0165	*
Turf algae - CCA		-3.805	-6.230	-1.379	0.0007	***
Turf algae - *Pocillopora* spp.		-0.976	-3.402	1.450	0.7071	ns
Response parameter: Pn:R	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
organism	3	107.2	35.7	5.221	3.60E-03	**
Residuals	44	301.2	6.8			
Tukey HSD		diff	lwr	upr	p adj	
CCA - *C. sertularioides*		-2.900	-5.752	-0.048	0.0450	*
Pocillopora spp. - *C. sertularioides*		-3.442	-6.295	-0.590	0.0123	***
Turf algae - *C. sertularioides*		-0.447	-3.299	2.405	0.9750	***
Pocillopora spp. - CCA		-0.543	-3.395	2.309	0.9567	*
Turf algae - CCA		2.453	-0.399	5.305	0.1145	***
Turf algae - *Pocillopora* spp.		2.995	0.143	5.848	0.0362	ns

2. Differences in oxygen fluxes comparing seasons

	Response parameter: Pn	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
	season	1	9.8	9.8	0.048	0.8267	ns
	Residuals	130	26448.6	203.5			
	for subsets of organisms						
Pocillopora spp.	season	1	175.7	175.7	4.693	0.0381	*
	Residuals	31	1160.5	37.4			
CCA	season	1	9.0	9.0	0.645	0.4282	ns
	Residuals	31	435.0	14.0			
Turf algae	season	1	177.9	177.9	0.646	0.4276	ns
	Residuals	31	8535.2	275.3			
C. sertularioides	season	1	10.0	10.0	1.327	0.2581	ns
	Residuals	31	234.1	7.6			
	Response parameter: Pg	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
	season	1	27.6	27.6	0.090	0.7652	ns
	Residuals	46	14074.9	306.0			
	for subsets of organisms						
Pocillopora spp.	season	1	120.9	120.9	2.233	0.1660	ns
	Residuals	10	541.6	54.2			
CCA	season	1	7.1	7.1	0.679	0.4293	ns
	Residuals	10	104.1	10.4			
Turf algae	season	1	412.9	412.9	1.924	0.1955	ns
	Residuals	10	2145.9	214.6			
C. sertularioides	season	1	14.8	14.8	0.997	0.3417	ns
	Residuals	10	148.3	14.8			
	Response parameter: R	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
	season	1	18.0	18.0	1.640	0.2068	ns
	Residuals	46	504.1	11.0			
	for subsets of organisms						
Pocillopora spp.	season	1	16.4	16.4	3.869	0.0776	ns
	Residuals	10	42.4	4.2			
CCA	season	1	18.1	18.1	4.143	0.0692	ns
	Residuals	10	43.7	4.4			
Turf algae	season	1	0.0	0.0	0.000	0.9852	ns
	Residuals	10	92.9	9.3			
C. sertularioides	season	1	0.1	0.1	0.122	0.7344	ns
	Residuals	10	4.4	0.4			
	Response parameter: Pn:R	Df	Sum Sq	Mean Sq	F value	Pr (>F)	
	season	1	36.2	36.2	4.469	0.0400	*
	Residuals	46	372.3	8.1			
	for subsets of organisms						
Pocillopora spp.	season	1	0.3	0.3	0.441	0.5217	ns
	Residuals	10	7.0	0.7			
CCA	season	1	12.4	12.4	5.989	0.0344	*
	Residuals	10	20.7	2.1			
Turf algae	UPW	1	27.1	27.1	1.529	0.2446	ns
	Residuals	10	177.0	17.7			
C. sertularioides	season	1	7.6	7.6	1.538	0.2433	ns
	Residuals	10	49.2	4.9			

Significance levels: * <0.05, ** <0.01, *** <0.001, ns: non-significant

Supplementary Table S3.2: Statistical results of linear models correlating oxygen fluxes to water parameters

1. Overall oxygen fluxes

Response parameter: Pn	log(Pn+1) ~ taxa + temperature + light + nutrients + DOC + taxa:temperature + taxa:DOC				
	Df	Sum Sq	F value	Pr(>F)	
taxa	3	29.379	69.823	< 2.2E-16	***
temperature	1	0.958	6.829	0.0107	*
light	1	2.193	15.637	0.0002	***
nutrients	1	1.173	8.365	0.0049	**
DOC	1	0.443	3.157	0.0793	ns
taxa:temperature	3	0.750	1.784	0.1568	ns
taxa:DOC	3	0.885	2.104	0.1060	ns
Residuals	82	11.501			
Response parameter: Pg	log(Pg+1) ~ taxa + light + DOC + POC + taxa:POC				
	Df	Sum Sq	F value	Pr(>F)	
taxa	3	10.259	99.851	5.76E-13	***
light	1	0.543	15.863	0.0006	***
DOC	1	0.389	11.344	0.0028	**
POC	1	0.005	0.134	0.7181	ns
taxa:POC	3	0.356	3.461	0.0337	*
Residuals	22	0.754			
Response parameter: R	log(R+1) ~ taxa + temperature + POC + taxa:temperature				
	Df	Sum Sq	F value	Pr(>F)	
taxa	3	8.340	34.501	2.22E-09	***
temperature	1	0.791	9.813	0.0041	**
POC	1	0.109	1.358	0.2541	ns
taxa:temperature	3	0.368	1.521	0.2316	ns
Residuals	27	2.176			

2. Organism-specific Pn

***Pocillopora* spp.**	log(Pn+1) ~ light + nutrients + DOC				
	Df	Sum Sq	F value	Pr(>F)	
light	1	1.103	6.978	0.0157	*
nutrients	1	0.337	2.130	0.1600	ns
DOC	1	1.070	6.766	0.0171	*
Residuals	20	3.162			
CCA	no model found				
Turf algae	log(Pn+1) ~ temperature + light + nutrients + DOC				
	Df	Sum Sq	F value	Pr(>F)	
temperature	1	1.033	7.322	0.0140	*
light	1	0.984	6.971	0.0161	*
nutrients	1	0.696	4.932	0.0387	*
DOC	1	0.164	1.159	0.2951	ns
Residuals	19	2.681			
C. sertularioides	log(Pn+1) ~ temperature + light + nutrients				
	Df	Sum Sq	F value	Pr(>F)	
temperature	1	0.685	13.684	0.0009	***
light	1	0.342	6.838	0.0142	*
nutrients	1	0.348	6.953	0.0135	*
Residuals	28	1.402			

Significance levels: * <0.05, ** <0.01, *** <0.001, ns: non-significant

4 Benthic community shift in an upwelling-exposed coral reef on the Pacific coast of Costa Rica

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Key words: coral reef - community dynamics - phase shift - upwelling - eastern tropical Pacific - Costa Rica - Gulf of Papagayo

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Abstract

Seasonal upwelling at the northern Pacific coast of Costa Rica offers the opportunity to investigate effects of pronounced changes in key water parameters on fine-scale dynamics of local coral reef communities. This study monitored benthic community composition at Matapalo reef (10.539°N, 85.766°W) by weekly observations of permanent quadrats from April 2013 to April 2014. Monitoring was accompanied by herbivore surveys and measurements of water temperature and nutrient concentrations. Findings revealed a shift from turf algae to hard coral dominance within the observed year. Cover of the coral *Pocillopora* spp. increased continuously from 22 to 51 %, while that of turf algae decreased from 63 to 24 %. Crustose coralline algae that were previously overgrown by turf algae increased with decreasing turf cover in June 2013, and slightly decreased with increasing coral cover over the year. The macroalga *Caulerpa sertularioides* covered substantial parts of the reef in April 2013, but disappeared after synchronized gamete release. Upwelling decreased mean water temperatures by 2.3 °C and increased mean phosphate and nitrate concentrations by 70 % and 270 % respectively from February to April 2014. This did not affect relative cover of benthic organisms, indicating that the reef community was acclimatized to pronounced seasonal changes in water parameters. Sea urchin abundances were high and controlled turf algal biomass. Rather than following a seasonal cycle, local reef communities are likely controlled by disturbance events such as warm periods, coral diseases, or harmful algae blooms with ensuing coral mortality followed by fast increases in coral cover.

4.1 Introduction

Coral reef benthic communities are shaped by a range of natural drivers, such as waves, water depth, reef habitat, temperature, nutrient concentrations and herbivory, as well as anthropogenic drivers including fishing, eutrophication and sedimentation. Recent research has mainly focused on the effects of anthropogenic disturbances on reef condition, while the ability of reef organisms to adjust to gradients in natural environmental conditions is equally interesting to study the ability of reef organisms to adapt to future changes. Long-term background physical conditions are known to drive spatial patterns in benthic community composition (Done 1992, Hughes et al. 2012, Williams et al. 2015). Although it is recognized that low- and high-frequency variations in conditions may also be influential drivers of coral reef benthic community composition and productivity (Leichter et al. 2003, Gove et al. 2015), it is not well known which parameters can determine benthic community composition on a fine temporal scale.

To understand the effects of variable environmental drivers on coral reef ecosystems it is useful to monitor ecosystems with a pronounced temporal variability in conditions, such as upwelling regions. Transport of subthermocline water to the surface in the form of coastal upwelling, large amplitude internal waves (LAIW) or internal bores decreases sea water temperature and increases nutrient concentrations in reef waters on different temporal scales ranging from minutes to several days (Leichter & Miller 1999, Leichter et al. 2005, D'Croz & O'Dea 2007, Schmidt et al. 2012). Previous studies in areas exposed to upwelling or LAIW mainly focused on spatial differences in benthic communities comparing exposed versus sheltered sites. Coral growth and reef development was thereby lower at sites exposed to upwelling in the Pearl Islands (Panamá) (Glynn & Stewart 1973) and to LAIW in the Similan Islands (Thailand) (Schmidt et al. 2012), suggesting adverse effects of upwelling on corals. On the other hand, upwelling may also increase symbiont densities and chlorophyll *a* concentrations in corals (Roder et al. 2011), lead to higher energy reserves by increased heterotrophic feeding (Roder et al. 2012) and benefit corals during high temperature stress (Wall et al. 2015). Studies on temporal differences in benthic community composition in response to upwelling are scarce. In the Colombian Caribbean, upwelling-induced temporal changes in community composition were found, but these were smaller than spatial differences caused by wave exposure (Eidens et al. 2015). Seasonal changes in the study by Eidens et al. (2015) were only assessed comparing one data point in upwelling and non-upwelling season each. In general, observations on a high temporal scale are often lacking in coral reef ecology. With observations in a weekly resolution, the present study aimed to advance the understanding of fine-scale dynamics on coral reefs.

We selected the Gulf of Papagayo at the northern Pacific coast of Costa Rica to investigate the question of how annual variability in environmental parameters affects coral reef com-

munities. A topographic depression in the lowlands of southern Nicaragua and northern Costa Rica allows strong winds to blow across from the Gulf of Mexico and the Caribbean during the northern hemisphere winter (McCreary et al. 1989, Amador et al. 2006, Willett et al. 2006), which on the Pacific side displace superficial water away from the coast and cause the shallow thermocline to break the surface (Fiedler & Talley 2006). This seasonal upwelling decreases mean seawater temperatures from around 28 °C between May and November down to 23 °C between December and April (Jiménez 2001a, Alfaro et al. 2012). During pronounced upwelling events, water temperature may drop by 8 - 9 °C (Alfaro & Cortés 2012) which is accompanied by drops in pH and oxygen concentration (Rixen et al. 2012) and peaks in nutrient concentrations, which seasonally promote the growth of fleshy macroalgae (Fernández-García et al. 2012, Cortés et al. 2014). Previous studies mention the potential limiting effects of upwelling on coral reefs in the Gulf of Papagayo (Glynn et al. 1983, Cortés 1997), but the effects of seasonal upwelling on fine-scale temporal dynamics in benthic community composition have not been investigated yet.

Therefore, this study analyzed the temporal variation in a reef community moderately exposed to upwelling in a weekly resolution over one year of monitoring. Observation of benthic community composition was accompanied by monitoring of herbivores (sea urchin abundance and fish biomass) and key water parameters (temperature and nutrient concentrations). The objectives of the study were to (1) observe the seasonality in benthic community composition, (2) identify the influencing biological and (3) environmental factors and (4) develop an ecological perspective for local coral reefs. Important key questions we aimed to answer within these objectives were: (i) which benthic groups benefit from seasonal changes in biotic and abiotic parameters? (ii) which parameter has the strongest effect on benthic community composition? and (iii) does the benthic community complete a seasonal cycle and return to the start conditions at the end of the year of observation?

4.2 Material and Methods

4.2.1 Study site

The study was conducted at Matapalo reef, located 12 km south of Culebra Bay in the Gulf of Papagayo at the northern Pacific coast of Costa Rica from April 2013 to April 2014. The reef framework at Matapalo in 3 - 9 m water depth is built by the branching corals *Pocillopora* spp. and stretches around 1.2 km from Punta Matapalito to the west end of Playa Matapalo (Fig. 4.1). Dead reef structure overgrown with turf algae alternates with healthy reef areas dominated by live coral cover. To the time of study, the benthic community in healthy reef areas was dominated by *Pocillopora* spp. (*P. elegans* and *P. damicornis*), crustose coralline algae (CCA) and turf algae communities. Turf algae communities existed in the form of fine

filamentous algae and cyanobacteria or in denser conglomerates with *Dictyota* spp. The green algae *Caulerpa sertularioides* was the only individually growing fleshy macroalga on the reef and covered large parts of dead reef framework in shallow areas and on the edges of reef patches. Single coral colonies of *Pocillopora* spp., *Pavona* spp. and *Psammocora* spp. and coral rubble could be found on sandy patches between the reef rock areas.

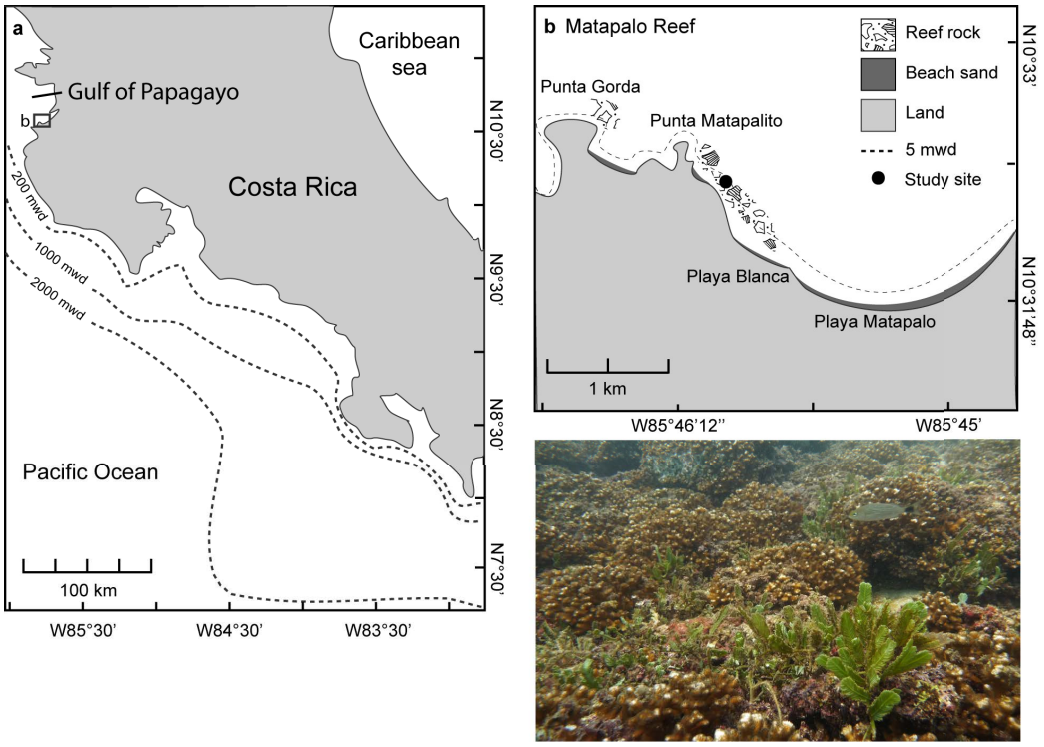

Figure 4.1: Study site. (a) Upwelling influenced Gulf of Papagayo at the northern Pacific coast of Costa Rica; (b) Location of study site at Matapalo reef. The photograph was taken at 5 m depth and shows the reef structure and dominant reef organisms.

4.2.2 Monitoring of benthic community composition

Monitoring took place on a healthy reef patch of around 600 m^2 (10°32'21.2"N, 85°45'57.9"W), 500 m north-west of Playa Blanca (Fig. 4.1b). Quadrats of 50 x 50 cm (n = 5) were permanently marked with iron stakes and repeatedly observed for changes in benthic coverage every week. The location of permanent quadrats was chosen by placing a 50 x 50 cm PVC frame alternately left and right every 2 m along a transect line parallel to the coast in 5 m water depth. For observation, the PVC frame with a 5 x 5 cm grid was placed over the stakes as a reference, and live coral, dead coral, CCA, turf algal, macroalgal, sand, rubble and sessile benthic invertebrate cover on the substrate was quantified from directly above the grid using SCUBA. Although the weekly quantification was done on a relatively

small area of the reef patch, results were confirmed by monthly chain surveys along permanently marked transects covering the whole reef patch (see below), which showed the same temporal patterns in community composition (C. Sánchez-Noguera, unpublished data).

4.2.3 Monitoring of herbivores

Transects of 10 m length (n = 5) were permanently marked with iron stakes parallel to the coast in 5 m water depth in about 3 m distance to the permanent quadrats. Surveys of sea urchins and fish were conducted monthly between 9:00 and 14:00 on all transects using SCUBA. Sea urchins of the species *Diadema mexicanum* and *Eucidaris thourasii* were counted in 1 m belts on both sides of the transect lines (total survey area = 100 m^2) from April 2013 to April 2014. Fish surveys were conducted from November 2013 to March 2014. During surveys, all individuals except cryptic species in 2.5 m belts on both sides of the transect lines (total survey area = 250 m^2) were identified to species level and assigned to size classes (5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm, 30-35 cm and 35-40 cm). Multiple swims (n = 3) with intervals of 5 min between swims were conducted on each transect in order to increase the precision of data for each transect. Biomass was afterwards calculated from mean length of each size class and species- or family-specific Bayesian length-weight relationship parameters available on FishBase (Froese & Pauly 2012).

4.2.4 Monitoring of water parameters

Monitoring of benthic community composition was accompanied by measurements of temperature with a Manta 2 Water Quality Multiprobe deployed directly on the reef substrate (recording over 1 - 6 hours in 4 min intervals) and weekly determination of inorganic nutrient concentrations. Water samples for nutrient measurements (500 mL) were taken in triplicate from directly above the reef surface within glass jars, filtered immediately through disposable syringe filters (pore size 0.45 µm) and stored cool for transportation. Ammonia (NH_4^+) was determined fluorimetrically within 24 h after sampling with a Trilogy® Laboratory Fluorometer/Photometer (Turner Designs) according to Holmes et al. (1999) and Taylor et al. (2007) (detection limit (LOD) = 0.023 µmol L^{-1}). Determination of phosphate (PO_4^{3-}) was conducted spectrophotometrically with the same device following the standard protocol of Murphy & Riley (1962) (LOD = 0.033 µmol L^{-1}). Sub-samples were kept dark and frozen until the end of the study period and were analyzed for nitrate (NO_3^-) and nitrite (NO_2^-) concentrations using a Thermo Scientific UV Evolution 201® photometer based on a method revised by García-Robledo et al. (2014) ($LOD_{(NO_2^-)}$ = 0.151 µmol L^{-1}; $LOD_{(NO_x)}$ = 0.162 µmol L^{-1}).

4.2.5 Statistics

Values in the text are means ± SE if not stated otherwise. Differences in fish and sea urchin abundances over time were tested with one way ANOVAs followed by Tukey post-hoc tests in SigmaPlot13 for Windows. Seasonality in environmental parameters and benthic community composition was examined with Principal Coordinate Ordinations (PCO) (Gower 1966) and tested by Permutation Multivariate Analyses of Variance (PERMANOVA) (Anderson 2001, Anderson et al. 2008) in PRIMER 6. Prior to analysis, weekly means of environmental parameters (temperature, PO_4^{3-}, NH_4^+, NO_3^-) were normalized and a resemblance matrix calculated using Euclidean similarity. The resemblance matrix of benthic community (cover of *Pocillopora* spp., dead coral, CCA, turf algae, *C. sertularioides*, sand, rubble and zoanthids) was calculated using Bray Curtis similarity. The fixed factors used for the analysis of data were (1) seasons with four levels (April 2013 - July 2013, August 2013 - October 2013, November 2013 - January 2014 and February 2014 - April 2014) and (2) months with 13 levels (months from April 2013 to April 2014). To test how well patterns in community composition correlated to patterns in environmental parameters, the function RELATE in PRIMER 6 was used, which tested matching of the resemblance matrices by Spearman Rank correlation.

4.3 Results

4.3.1 Benthic community composition

Weekly observations of permanent quadrats revealed a major shift from turf algae to hard coral dominance within the observed year. Cover of the hard coral *Pocillopora* spp. increased continuously from 22 % in April 2013 to 51 % in April 2014 (Fig. 4.2a). Turf algae initially covered around 60 % of the substrate but decreased to 35 % within two weeks in June 2013. The drop in turf algae cover increased the relative cover of CCA from 15 to 30 % in June, as turf algae were covering crustose algae on the substrate before. CCA cover remained around 30 % until January 2014, when it decreased slightly coincident with increasing coral cover (Fig. 4.2a). The macroalga *Caulerpa sertularioides* covered 3 % of the substrate in permanent quadrats in April 2013 but decreased to 0.1 - 0.5 % within 3 weeks. Macroalgal cover again increased temporarily to 5 % in August 2013 and 2.5 % in March 2014 (Fig. 4.2b). The drop in *C. sertularioides* cover from April to May 2013 could be observed in a more pronounced way in the whole reef (drop from 15 to 1 % cover, C. Sánchez-Noguera, unpublished data) and was associated with whitening of the macroalgal's stolons and fronds. Sand and rubble in permanent quadrats increased from around 0.5 % substrate cover between April and October 2013 to 1.5 % and around 4 % respectively in March and April 2014 (Fig. 4.2b). Zoanthids were the only sessile invertebrates observed (0.0 to 0.2 %).

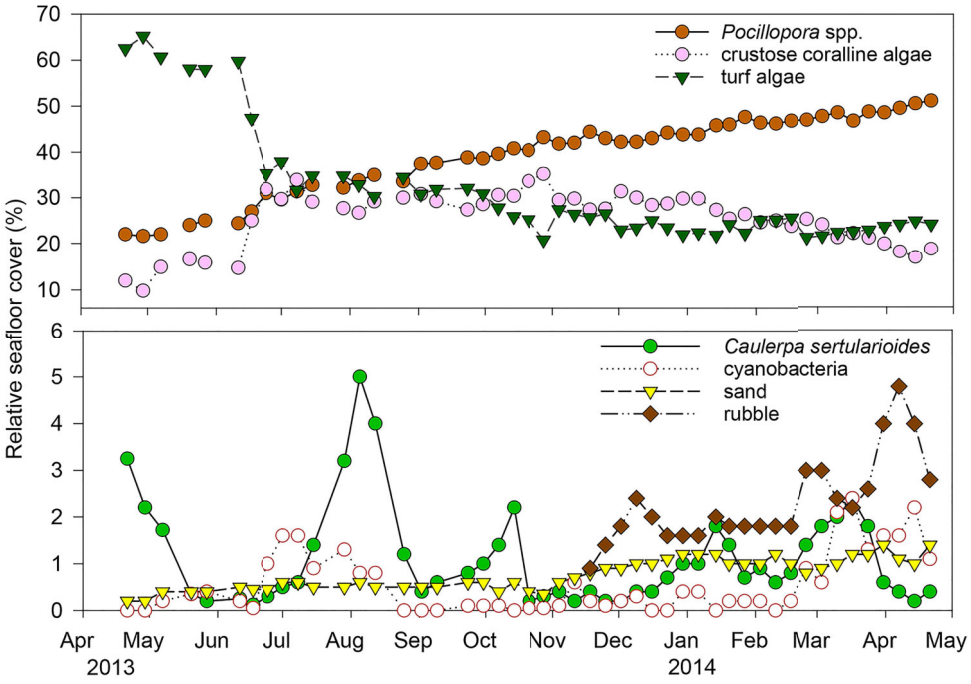

Figure 4.2: Temporal changes in coral reef community composition. Displayed are mean proportional coverages of benthic organisms or substrates in permanent quadrats of 50 x 50 cm (n = 5) from April 2013 to April 2014 in a weekly resolution. Note the different scales of y-axes.

Multivariate analyses illustrated the pronounced shift in benthic community composition over the study period (Fig. 4.3). From April to October 2013 the community shifted along PCO1, which explained 82 % of the total variance in the data and was positively correlated with cover of *Pocillopora* spp., and negatively with turf algae. From October 2013 to April 2014 the composition shifted further along PCO2, which explained 17.4 % of the total variance and showed a positive correlation to rubble and a negative correlation to CCA. Differences in community composition were significant between seasons (Pseudo-F(3,43) = 35.785, p(perm) = 0.001, perms = 997) and months (Pseudo-F(12,34) = 47.848, p(perm) = 0.001, perms = 998).

4.3.2 Herbivore community

Sea urchin abundances in the reef averaged 5.31 ± 0.36 ind. m^{-2} for *Diadema mexicanum* and 0.16 ± 0.03 ind. m^{-2} for the pencil sea urchin *Eucidaris thourasii* (Fig. 4.4a). Individuals of *Astropyga pulvinata* and *Tripneustes depressus* occasionally occurred on the reef but were rarely counted during surveys. Abundances of *D. mexicanum* and *E. thourasii* did not change significantly during the study period (F(12,52) = 0.991, p = 0.470 and F(12,52) = 1.336, p = 0.228 respectively).

Total fish abundance was 3-fold higher in December 2013 compared to other months,

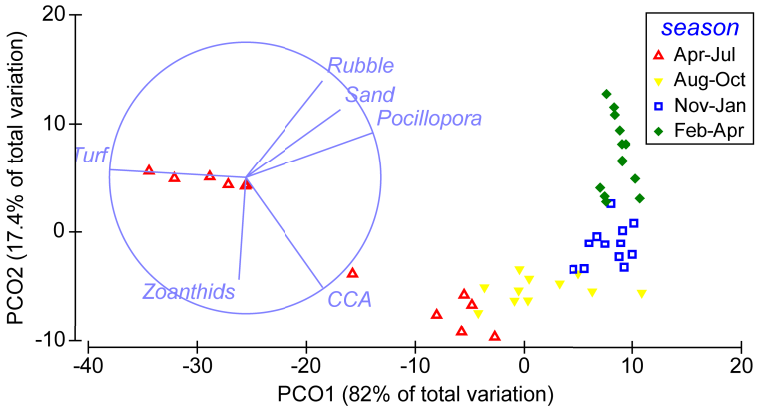

Figure 4.3: Time shift in benthic community composition. Weekly sampling data from April 2013 to April 2014 were grouped by the factor season. The distance between data points reflects their similarity in benthic community composition (close = similar) and the shift along axes can be assigned to changes in benthic cover types (arrows). PCO1 correlates positively to cover of *Pocillopora* spp., sand, rubble and CCA and negatively to turf algae. PCO2 correlates positively to rubble and sand and negatively to CCA and zoanthids. Only variables with $r > 0.5$ are displayed.

which was due to high abundances of *Chromis atrilobata* (Fig. 4.4b). As these damselfish are rather small, the high abundances did not affect the respective fish biomass comparing values with or without damsels in December 2013 ($t8 = 0.958$, $p = 0.366$). Total fish biomass on the reef was significantly elevated in November and December 2013 compared to the following three months (Fig. 4.4c; $F(4,20) = 14.729$, $p < 0.001$).

Parrotfish were the most abundant roving herbivores at the study site, while surgeonfish were sometimes observed on the reef during diving, but hardly counted during surveys. Parrotfish abundances were 3.7-fold higher in December 2013 and 3.2-fold higher in March 2014 compared to the rest of the survey period (Fig. 4.4b). Small individuals below 10 cm were observed in December 2013 and January 2014, while large individuals above 25 cm were mainly observed in December 2013 (Fig. 4.4d), resulting in significantly higher parrotfish biomass in December 2013 than in November 2013, January 2014 and February 2014 (Fig. 4.4c; $F(4,20) = 7.603$, $p < 0.001$). A statistical correlation of fish abundance or biomass and benthic community composition was not possible due to missing fish data during the first half of the study period.

4.3.3 Water parameters

Short drops in temperature by around 2 °C occurred at Matapalo reef in June, October and December 2013 (Fig. 4.5a). More pronounced and longer lasting cooling events, coupled with increased nutrient concentrations, occurred between February and April 2014, which is from now on referred to as the 2013/2014 upwelling season. Average water temperatures during that upwelling season decreased from 28.5 ± 0.1 °C to 26.2 ± 0.6 °C, while average

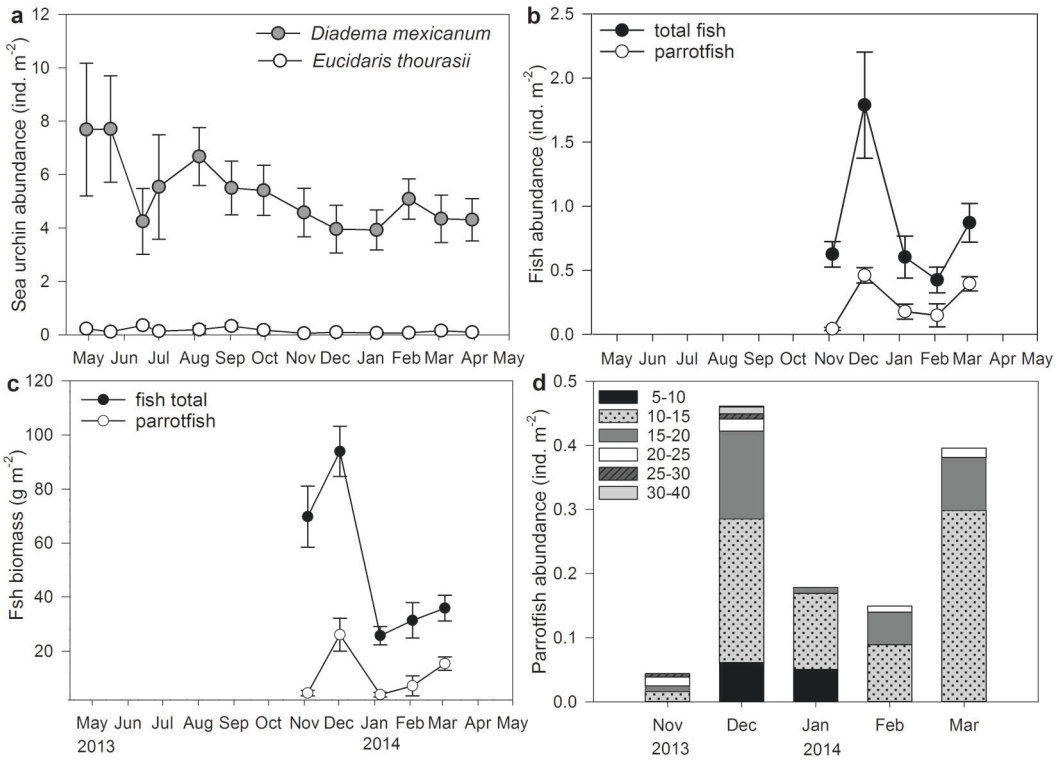

Figure 4.4: Changes in sea urchin and fish community. Displayed are mean ± SE (n = 5) abundances of (a) sea urchins and (b) fish, (c) fish biomass calculated from abundances and mid length of size classes and (d) relative abundance of parrotfish size classes (in cm) in permanent belt transects (n = 5) from April 2013 to April 2014 in a monthly resolution.

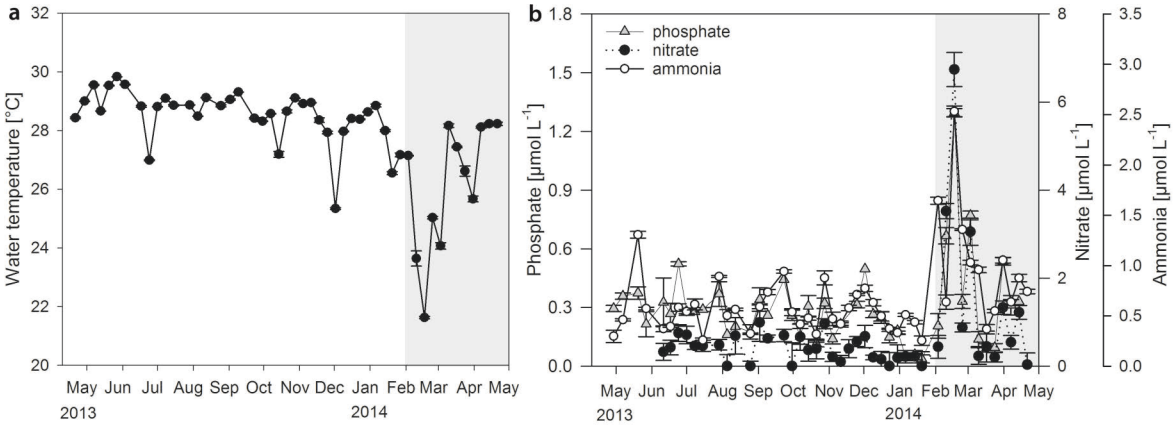

Figure 4.5: Changes in temperature and nutrient concentrations. Displayed are mean ± SE values for (a) water temperature (measured over 1 - 6 h in 4 min intervals) and (b) nutrient concentrations (n = 3) directly above the reef substrate from April 2013 to April 2014 in a weekly resolution. Shading indicates upwelling season.

PO_4^{3-}, NH_4^+ and NO_3^- concentrations increased by 70, 80 and 270 % respectively. During strongest upwelling events, mean daily seawater temperatures dropped by 7 °C to minima of 22 °C and nutrient concentrations increased 5-, 4- and 16-fold to maxima of 1.3 µmol PO_4^{3-} L^{-1}, 2.5 µmol NH_4^+ L^{-1} and 6.7 µmol NO_3^- L^{-1} respectively (Fig. 4.5b).

According to the PCO analysis, the variance of environmental conditions at Matapalo from April 2013 to April 2014 was mainly explained along PCO1 (79.3 % of total variation), which highly correlated with temperature (r = -0.86), PO_4^{3-} (r = 0.93), NH_4^+ (r = 0.83) and NO_3^- (r = 0.95) (Fig. 4.6). Environmental conditions were significantly different between seasons (Pseudo-F(3,43) = 16.68, p(perm) = 0.001, perms = 998) and months (Pseudo-F(12,34) = 2.7984, p(perm) = 0.006, perms = 997). The temporal pattern in environmental parameters did not correlate to the pattern in community composition (Rho = 0.029, p(perm) = 0.332, perms = 999) and therefore did not explain any variance in the benthic community data.

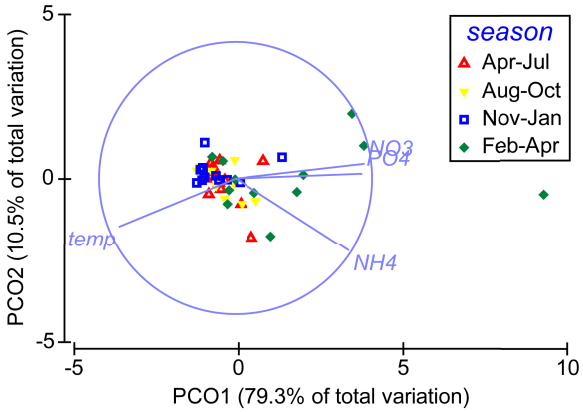

Figure 4.6: Temporal pattern in environmental parameters. Weekly sampling data from April 2013 to April 2014 were grouped by the factor season. The distance between data points reflects their similarity in environmental conditions (close = similar) and the separation along axes can be assigned to changes in environmental parameters (arrows). Sampling points in upwelling season are separated from the rest along PCO1, correlating highly with temperature (r = -0.86), PO_4^{3-} (r = 0.93), NH_4^+ (r = 0.83) and NO_3^- (r = 0.95).

4.4 Discussion

This study is the first to describe the variability in benthic coral reef communities in response to seasonal upwelling in such temporal resolution. Findings hint to a highly dynamic benthic community, which was however not directly influenced by the observed seasonality in environmental conditions during the study period.

4.4.1 Benthic community composition

In terms of relative abundance, the scleractinian coral *Pocillopora* spp. benefited most from prevalent conditions in the year of observation, followed by CCA, while turf and fleshy macroalgae declined. The reef community did not follow a seasonal cycle with repeated dominance of algae in the upwelling season, but live coral cover increased continuously over the observation year, shifting the observed reef patch from turf algae to coral dominance.

An increase in absolute coral cover is important to retain a coral-dominated state in the face of disturbances and has been used in most studies demonstrating reef recovery (Hughes et al. 2010, Graham et al. 2011). For reefs dominated by fast growing coral species, the recovery of coral cover may even match the rate of benthic community reassembly (return to original composition) after disturbances (Johns et al. 2014). Graham et al. (2011) reviewed recovery rates of absolute coral cover and found mean annual rates of 3.56 % (with a range from 0.13 to 12.49 %). The annual increase rate of almost 30 % observed during our study is among the fastest reported in the scientific literature. A similar annual increase rate of live coral cover by >40 % was only observed in the Great Barrier Reef following coral bleaching and a subsequent bloom of the seaweed *Lobophora variegate* (Diaz-Pulido et al. 2009). In that study, unusually rapid regrowth of the branching coral *Acropora* by 100 - 200 % within 6 - 12 months was attributed to fast tissue regeneration from relatively small amounts of live tissue, high competitive ability of the corals, and a seasonal dieback in the blooming seaweed. Growth over existing skeleton seem to offer an energetically efficient and rapid mechanism for coral cover increase by limiting the calcification required for regrowth (Diaz-Pulido et al. 2009). We however have to be aware that reef recovery cannot be measured based on coral abundance or growth rates alone, but should include measures of biodiversity, recruitment rates and colony size distribution. The increase in coral cover at our study site followed a seasonal reduction in algal cover and did not involve new coral recruitment (no coral recruits on settlement tiles, Roth et al. 2015), but was driven by the expansion of remaining live tissue over already existing dead skeleton and high linear growth rates. Linear growth rates for *P. damicornis* and *P. elegans* in the Gulf of Papagayo are higher than reported anywhere else in the eastern tropical Pacific (up to 67 ± 9 mm yr^{-1} and 52 ± 10 mm yr^{-1}, respectively, Jiménez & Cortés 2003) which was related to high nutrient availability during upwelling (Glynn 1977, Wellington & Glynn 1983, D'Croz & O'Dea 2007). Upwelling inorganic nutrients may enhance the photosynthesis of coral symbionts and the concentration of plankton serving as prey for heterotrophic feeding (Roder et al. 2010, 2011). Increased photosynthesis and feeding rates during upwelling may therefore offset the negative impacts of cold waters and enable the corals' constantly high expansion rates observed (Manzello 2010).

During their rapid expansion, corals in the present study were able to successfully compete with CCA and turf algae, even in periods of high nutrient input. Competitive superiority of corals over algae has been demonstrated before (Meesters et al. 1997, McCook 2001, Diaz-Pulido et al. 2009), but most studies observing coral-algae interactions have emphasized the dominance of algae over corals (e.g. Tanner 1995, Quan-Young & Espinoza-Avalos 2006, Hughes et al. 2007). Turf algae are able to overgrow branching corals at high rates and increased nutrient concentrations often exacerbate their competitive superiority (Vermeij et al. 2010, Haas et al. 2010). Besides turf algae, macroalgae may also have detrimental effects of corals. The invading green alga *Caulerpa sertularioides* is spreading in the Gulf of Papagayo since 2001, smothering and killing corals (Fernández & Cortés 2005, Cortés et al. 2010). In the present study, *C. sertularioides* covered large parts of the reef framework in April 2013, but disappeared almost entirely from the reef structure within four weeks, after the stolons and fronds of the macroalga turned white. Fernández-García et al. (2012) observed the same phenomenon with a decrease of 40 % in algal coverage in Culebra Bay in February 2004 and 2005. They associated the whitening of fronds with synchronous sexual gamete release, possibly triggered by changes in environmental conditions after the upwelling peak, when cover and density of the algae had been highest.

4.4.2 Biotic drivers

Herbivores in coral reef ecosystems have long been recognized to serve as important top-down control on the establishment and growth of algal communities (e.g. Ogden & Lobel 1978, Lewis 1986, McCook 1999). Changes in herbivore densities can therefore largely influence the community composition in reefs (e.g. Hughes 1994, Bellwood et al. 2004). On the studied reef patch, herbivore abundances were consistent while patterns of algal cover revealed temporal changes. High abundances of sea urchins and herbivorous fish were likely able to control algal biomass over the year and to reduce turf algae cover after an upwelling induced bloom in the beginning of 2013.

Parrotfish were the main roving herbivore at the study site and individuals below 10 cm indicated successful recruitment and the importance of the studied reef as fish nursery. Comparable data on parrotfish biomass from eastern tropical Pacific reefs are not available, but biomass found during this study were in the range of mean values for the Indo Pacific (13.1 ± 2.4 g m^{-2}, Roff & Mumby 2012). The decrease in algal cover over time, and results from caging experiments at the study site (Roth et al. 2015) suggest that herbivorous fish were able to control algal growth, even during nutrient-rich upwelling season. Fish were observed to graze on turf algae, but not on *C. sertularioides*, which may primarily be bottom-up controlled.

Besides from herbivorous fish, grazing sea urchins such as *Diadema* can limit algal dom-

inance and thereby increase reef resilience, as it was evident in the Caribbean (Lessios 1988, Knowlton 1992, Hughes 1994). Models showed that even a moderate abundance of 1 ind. m^{-2} may be sufficient to drive coral population recovery after disturbances (Roff & Mumby 2012). *Diadema mexicanum* abundances of around 5 ind. m^{-2} at the study site are therefore likely to contribute substantially to the removal of algae. Grazing control is especially important to reduce algae abundance after a seasonal bloom, when algal growth temporarily exceeds grazing rates. By considerably reducing turf algae cover in June 2013, *D. mexicanum* likely uncovered underlying crustose coralline algae and thereby facilitated increases in coral cover. High abundances of *Diadema* spp. can however also damage a reef by extensively eroding the carbonate substrate (e.g. Ogden 1977, Glynn 1988a, Eakin 2001). Indeed, cover of sand and rubble in permanent quadrats increased during the study period, and the reef framework was quite thin despite fast coral growth (approximately 40 cm thick on the studied patch). Abundances of sea urchins were above the threshold of 3 ind. m^{-2} predicted to shift the reefs in Culebra Bay from a positive to a negative carbonate balance due to high erosion rates (Alvarado et al. 2012). Bioerosion exceeding carbonate deposition has already affected other reefs of the eastern tropical Pacific (Glynn 1988a, Colgan 1990, Eakin 1996, Reaka-Kudla et al. 1996, Alvarado et al. 2012) and is therefore a realistic threat to Matapalo reef.

4.4.3 Abiotic drivers

Coral reefs prefer warm and oligotrophic conditions for optimal growth (Muscatine & Porter 1977, Kleypas et al. 1999). Due to the pronounced decrease in water temperature and the increase in nutrient concentrations during upwelling we expected an increasing competition between corals and macroalgae between December 2013 and April 2014. Instead, algae cover was low and rapid coral growth continued throughout upwelling season, likely supported by high herbivorous feeding pressure. Temperature and nutrient concentrations during the year of observation did therefore not directly drive the variability in benthic community composition.

While corals in the present study were not affected by the decrease in water temperature between February and April 2014, several studies in the gulfs of Papagayo and Panama reported limited reef building due to upwelling (Glynn & Stewart 1973, Guzmán & Cortes 1993) and bleaching and mortality in *Pocillopora* spp. following water temperatures below 15 °C (Glynn & Stewart 1973, Glynn et al. 1983, Glynn & D'Croz 1990, Jiménez 2001a). The mean seawater temperature in February 2014 was in the range of data from Culebra Bay in the same water depth between 1998 and 2006 (Jiménez et al. 2010), and minimum water temperatures of 20.1 °C during our study period were well above the cold water bleaching threshold proposed above. The observed drops in temperature by up to 7 °C in February

2014 are a challenge to most organisms, but benthic organisms at the study site were obviously well adapted to these pronounced and fast changes in conditions.

Cover of the macroalga *C. sertularioides* was highest in April 2013, which likely represented the end of the upwelling season 2012/2013. Cover and density of the macroalgae in near-by Culebra Bay was highest during the upwelling peaks of 2004 and 2005 (Fernández-García et al. 2012), suggesting that the reproductive cycle and coverage of *C. sertularioides* may primarily be nutrient controlled. A strong response to nutrient addition was also observed in Panama, where the algae occurred in off-reef populations but bloomed onto the near-by reefs when nutrient input increased during La Niña conditions (Smith et al. 2010). However, macroalgal cover at Matapalo did increase only moderately during upwelling season 2013/2014 and did not reach coverage of the previous year, despite high availability of nutrients. The reproductive cycle of *C. sertularioides* may therefore be longer than one calendar year, or nutrient supply was not elevated long enough to induce a renewed macroalgal bloom.

In contrast, turf algae recruiting to newly available substrate benefited from elevated nutrient concentrations during upwelling. Cover and biomass of turf algae on short-term exposed terracotta settlement tiles almost doubled in February and March 2014 (Roth et al. 2015). Due to their high surface to volume ratio, turf algae may take up nutrients from pulse events, such as upwelling, faster than other macroalgae (Carpenter 1990) and episodic nutrient input may therefore strongly affect the temporal pattern of turf algal production (Russ & McCook 1999). In the established reef community however, relative turf algae cover did not increase during upwelling season. The large herbivore community and highly competitive corals were obviously able to offset the promotion of algae by nutrients.

4.4.4 Ecological perspective

Reefs in the eastern tropical Pacific are considered to exhibit low resilience due to limited biological diversity, little sexual recruitment and slow reef recovery (reviewed in Cortés 1997, 2011). The present study indicates that local reef resilience may be higher than formerly suggested, with high resistance to seasonal changes in environmental parameters and a velocity of coral cover increase that was rarely reported before. The following perspectives have limitations as they are based on one calendar year of data and anecdotal evidence from previous studies, but nevertheless improve the understanding of ecosystem functioning in the marginal reefs of the eastern tropical Pacific.

The continuous increase in live coral cover over the studied year suggests that the investigated reef patch was recovering after a disturbance event in the past. Occurrence of mass coral mortality have been reported along the coast of Costa Rica and were attributed to siltation (Jiménez 2001b), harmful algal blooms (Guzmán et al. 1990) and El Niño warm-

ing events (Glynn 1990, Guzmán & Cortés 2001, Jiménez et al. 2001). These disturbances can decrease coral cover in local reefs, which may then recover until the next disturbance. The reefs around Matapalo were almost completely dead in 1978 (Glynn et al. 1983). Any possible recovery was probably prevented by the 1982/83 El Niño event, which annihilated most reefs in Panama and Costa Rica (Glynn 1984, 1988b, Cortés & Jiménez 2003), followed by reef framework destruction by echinoid bioerosion (Glynn 1988a). In 1988, the reefs around Matapalo were still largely dead, but most of them recovered substantially over the next 20 years (C. Jiménez et al., unpublished data). While some reefs in the Gulf of Papagayo suffered from the 1997/1998 El Niño (Jiménez et al. 2001, Cortés et al. 2010), coral cover at Matapalo reef continued to increase until 2007, when live coral cover in 5 - 7 m depth was 60 - 80 % (C. Jiménez, unpublished data). The reef started to deteriorate in 2007 and collapsed in 2010 (26 % to 4 % absolute live coral cover) due to warm seawater temperatures over several months, coinciding with extensive macroalgal blooms (C. Jiménez, unpublished data; Méndez 2014). In January 2012, >50 % of coral colonies in some areas of Matapalo reef were affected by large scale tissue ablation, possibly caused by a coral disease (Wild et al. 2014). By the time of our study, the observed patch of Matapalo reef seemed to be in a state of recovery, at least concerning live coral cover. However, this was not true for all parts of the 1.2 km long reef. Furthermore, a fast growing coral not always indicates a healthy and resilient coral (Wooldridge 2014), and the repeated mortality events over the last decades prevented the coral community from increasing in diversity or developing to a resistant structure that can withstand erosion after death (Colgan 1990). High abundances of sea urchins together with poor cementation of eastern tropical Pacific corals may therefore reduce the stability of local reefs (Cortés 1997, Manzello et al. 2008). As maintaining reef framework integrity is equally important as coral growth and recruitment in the recovery process after disturbances (Endean 1976, Baker et al. 2008), local reefs will remain sensitive to natural and anthropogenic disturbances, despite high coral growth rates.

In conclusion, coral reefs in the Gulf of Papagayo seem resistant to upwelling conditions, but sensitive to other disturbance events. Multiannual catastrophic drivers followed by recovery may therefore be of higher importance shaping the benthic communities in the reefs of the Gulf of Papagayo than seasonal changes in environmental conditions. The fate of the reefs along the Pacific coast of Costa Rica will thus depend on the frequency and nature of disturbances and the prevailing conditions in the reef that facilitate or impede recovery. In this regard, efforts should be made to reduce siltation from road and infrastructure construction and nutrient input from untreated waste water, which may increase the occurrence of harmful algae blooms (Anderson et al. 2002, Heisler et al. 2008), coral diseases (Bruno et al. 2003, Sutherland et al. 2004) and abundances of internal bioeroders (Hallock & Schlager 1986, Holmes et al. 2000, Chazottes et al. 2002). Regulations for fishing could furthermore help to retain the healthy herbivore community in the reef ecosystem, which

may compensate for disturbance effects on the reefs (Ghedini et al. 2015, Graham et al. 2015).

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5 Effects of simulated overfishing on the succession of benthic algae and invertebrates in an upwelling-influenced coral reef of Pacific Costa Rica

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Abstract

Overfishing and nutrient enrichment are among the major local stressors to coral reefs worldwide, as they can alter the benthic reef community by promoting fast growing algae and bioeroders. The northern coast of Pacific Costa Rica is strongly influenced by seasonal upwelling events that naturally increase nutrient concentrations between December and March. This study therefore investigated the combined effects of simulated overfishing and naturally increased nutrients on benthic community composition and succession on settlement tiles over a period of 24 weeks (October 2013 until March 2014) using exclusion cages deployed in a coral reef in the Gulf of Papagayo. Tile cover of functional groups and development of organic C and N on light-exposed and shaded tiles were assessed. Results revealed that the exclusion of fish significantly increased the development of organic C and N and decreased the C/N ratio on light-exposed tiles. Large filamentous algae (>2 mm), fleshy macroalgae and the colonial ascidian *Didemnum* sp. (Savigny 1816) (up to 80 % tile coverage) dominated light-exposed and shaded tiles. A significant peak of filamentous algae growth and associated organic C and N increases occurred on light-exposed tiles throughout all treatments in February, when nutrient concentrations were elevated. These results suggest that both herbivore exclusion and natural eutrophication have a strong influence on the benthic reef community composition and its early succession patterns. The presence of *Didemnum* sp. and turf algae could represent good early warning bioindicators for local overfishing and eutrophication and may therefore be included in management and monitoring strategies.

5.1 Introduction

Many coral reefs around the world suffer from the combined effects of elevated nutrient concentrations and depleted fish stocks, which may result in pronounced changes in the benthic community composition (Burke et al. 2011). Recent studies have shown that not only filamentous turf algae and fleshy macroalgae are major competitors to corals (Hughes 1994), but that also sponges, colonial ascidians and other sessile invertebrates successfully compete for space (reviewed in Chadwick & Morrow 2011, Glynn & Enochs 2011).

Herbivorous fish play a crucial role in preconditioning coral reefs to allow for a successful coral recruitment and recovery (Bellwood et al. 2004). Their grazing activity limits turf- and macroalgae growth and therefore not only decrease coral-algae interactions but also opens space for crustose coralline algae (CCA) (Mumby 2009). The latter can facilitate the settlement of coral larvae by chemical cues (Heyward & Negri 1999, Harrington et al. 2004, Ritson-Williams et al. 2010). Additionally, a loss of herbivores attributable to fishing activities may result in increased growth of fleshy algae and therefore a loss of hard coral cover due to competition (e.g. McCook et al. 2001, Burkepile & Hay 2009, Smith et al. 2010). Subsequently, coral reefs may face a reduction of structural complexity (reviewed in McCook et al. 2001), which provides refuge also for invertebrate predators such as *Balistidae*, *Labridae* and *Haemulidae* (McClanahan et al. 1999). Bioeroders like sponges and ascidians generally comprise only a minor part of the benthic reef community (Glynn & Enochs 2011); nevertheless, they can compete successfully with scleractinian corals due to their fast growth and high reproduction rates, or the use of allelochemicals (Bak et al. 1981, Sawada et al. 2001, López-Victoria et al. 2006, Loh et al. 2015). The proliferation of benthic invertebrates or bioeroders is often triggered by changes in environmental conditions (e.g. decreased predation pressure or increased food availability) (Chadwick & Morrow 2011).

A second local stressor is the over-enrichment with nutrients in coastal waters. Scleractinian corals are adapted to oligotrophic coastal waters (Muscatine & Porter 1977). Some of the direct negative effects of high nutrient concentrations include a reduction in calcification rates (Ferrier-Pages et al. 2000), combined with limited coral growth (Fabricius et al. 2013) and a decrease in the reproduction activity (Loya et al. 2004). Eutrophication may also be tightly linked to the deleterious effects of coral bleaching (Wiedenmann et al. 2012) and an increased susceptibility to coral diseases (Thurber et al. 2014). Furthermore, elevated levels of nitrate and phosphate may promote the growth of benthic as well as planktonic algae (McClanahan et al. 2007). As a source of food, the increased availability of organic matter in the water column can additionally favor filter feeders, which are not physiologically inhibited by higher concentrations of nutrients (Bak et al. 1996, Ward-Paige et al. 2005).

Coral reefs at the northern coast of Pacific Costa Rica are exposed to highly dynamic

environmental conditions. Seasonally elevated nutrient concentrations due to coastal upwelling (Stumpf & Legeckis 1977, Clarke 1988) and a highly developed fishing industry challenge the present reefs (Mathiesen 2012). Strong wind jets channeled through a mountain gap in the Central American cordillera between December and April (McCreary et al. 1989, Romero-Centeno et al. 2007) displace surface water masses away from the coast, which are then replaced by colder and denser water from the depth (Bakun 1990). Primary productivity is high during upwelling season when nutrient rich water masses are welled up to the surface (Small & Menzies 1981). Furthermore, marine ecosystems in this area have to cope with strong impacts by local fisheries. Almost 80 % of the landings derive from artisanal fisheries, which target for reef and coastal fish species (Wehrtmann & Nielsen-Muñoz 2009) to meet the high demand of fish products for the tourism sector (Salas et al. 2011).

Even though studies have analyzed the combined effects of human induced eutrophication and overfishing on benthic algae growth, these investigations have almost exclusively been carried out in the Caribbean and the Red Sea (e.g. Smith et al. 2010, Rasher et al. 2012, Burkepile et al. 2013, Jessen et al. 2013). Additionally, most studies have only considered the impacts on the algal community, but little is known about the influences on invertebrate recruitment in this context (e.g. Abelson et al. 2005, Jessen et al. 2014). Furthermore, there are no studies available, how natural enhanced nutrient concentrations due to coastal upwelling may influence the benthic community composition and succession on tropical coral reefs. However, in order to sustain coral reef systems worldwide and to implement protecting management strategies, it is necessary to get a detailed understanding of the respective ecosystem (Hoegh-Guldberg et al. 2007, Daily et al. 2009). This study thus for the first time investigated the combined effects of simulated overfishing and natural seasonal eutrophication on the composition and succession of benthic algae and sessile invertebrate communities in a Pacific coral reef along the American continent. Fish exclusion cages with settlement tiles and the natural effects of coastal upwelling were used to: (1) assess the impact of simulated overfishing on in situ succession of benthic algae and invertebrates and (2) determine the effects of changing nutrient concentrations due to coastal upwelling on settling succession and composition of benthic algae along with invertebrates on a temporal scale.

5.2 Material and Methods

5.2.1 Study site

The study was carried out from October 2013 until March 2014 (duration = 24 weeks) in a patch reef located in the Gulf of Papagayo at the Northern Pacific coast of Costa Rica (N10°32'18.6" , W85°45'54.4") (Fig. 5.1). Matapalo Reef is located southwest of the well-

studied bay Bahía Culebra (reviews by Cortés 2012a, b). The reef is situated in close distance to the shore (approximately 20 - 30 m), in water depth of 5 to 7 m, depending on the tide. It is dominated by the branching hard coral *Pocillopora* spp. The Gulf of Papagayo experiences seasonal coastal upwelling that usually takes place between December and March (Jiménez 2001).

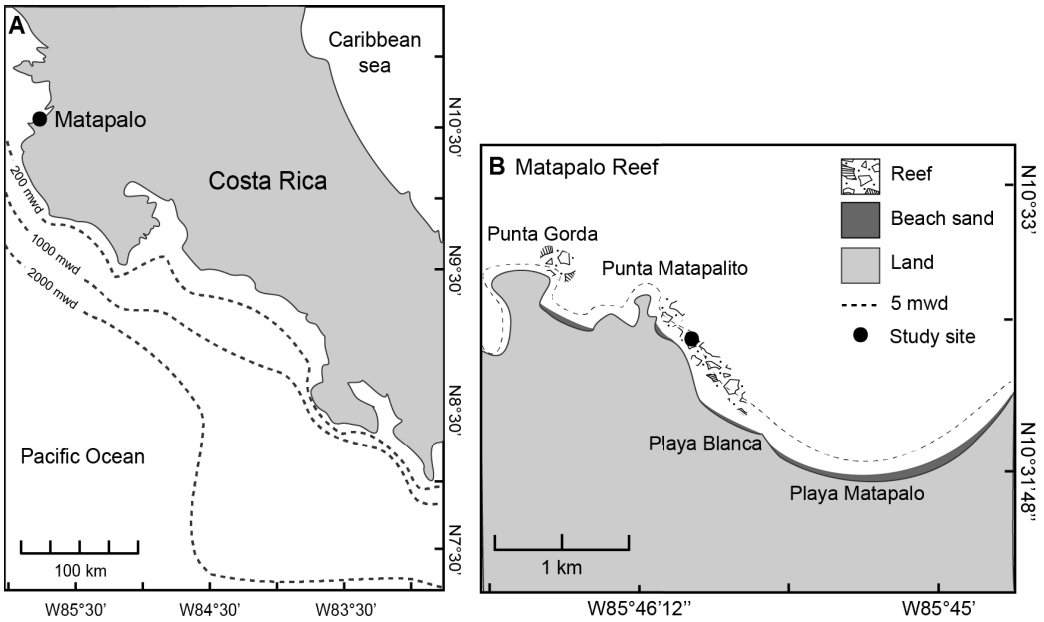

Figure 5.1: Maps of the Pacific coast of Costa Rica (A) and the study site Matapalo Reef (B). Map (A) indicates the location of the study site Matapalo Reef at the Northwestern Pacific coast of Costa Rica. Map (B) shows the location of the experimental set-ups.

5.2.2 Nutrient concentration measurements

Water samples were taken in triplicates directly from above the reef over the total study period of 24 weeks in a biweekly resolution. Concentrations of ammonium (NH_4^+), nitrate (NO_3^-) and phosphate (PO_4^{3-}) were determined. Samples were filtered through syringe prefilters and analyzed directly for concentrations of NH_4^+ and PO_4^{3-} using a Trilogy® Laboratory Fluorometer/Photometer (Turner Designs) for fluorometric analysis of ammonia and spectrophotometric determination of phosphate according to Murphy & Riley (1962). A part of the samples was frozen for determination of nitrite and nitrate using a method with the reduction of nitrate by vanadium(III) and a Photometer Thermo Scientific UV Evolution 201®. Chlorophyll *a* (chl *a*) concentrations were measured by filtering 3 L of seawater on pre-combusted filters (particle retention 1.6 µm), which were then incubated in 10 mL 90 % Acetone for 24 h at 4 °C before analyzed with a spectrophotometer.

5.2.3 Enumeration of fishes

Visual surveys of fish were carried out using underwater fish census methods described by Green & Bellwood (2009). Five transects with a length of 10 m each (n = 3 long-swims/ replicate) were observed monthly from November 2013 to March 2014 to investigate abundance, biomass and size classes of the fish community. The surveys were conducted between 9 am and 12 pm, 2.5 m left and right of the transect lines, surveying a total area of 250 m^2. All individuals ≥ 5 cm were counted and grouped in one of 6 size classes (5-10 cm, 10-15 cm, 15-20 cm, 20-25 cm, 25-30 cm and 30-40 cm). Cryptic species were not included in the surveys. Biomass estimations were calculated using known length-weight relationships (LWR) for fishes: The weight in grams (*W)* of a fish can be predicted by its fork length in cm (*L*) by using the formulae $W = aL^b$ (Froese et al. 2013). Parameters *a* and *b* are compiled at FishBase (Froese & Pauly 2009) for most species. If parameters were not available for single species, a higher taxonomic rank (e.g. family) was chosen. The mid value of each size category was used for the biomass estimation (e.g. 17.5 cm for size category 15-20 cm). Fish diversity was calculated for each observation day using the Shannon-Wiener index (Shannon 2001). Fishes were categorized as carnivore or herbivore, according to their ability to remove benthic algae (information taken from Froese & Pauly 2009). Due to their potential positive effect on algae growth through gardening and their territorial behavior (Hoey & Bellwood 2010), damselfish were not classified as herbivores in this study.

5.2.4 Experimental cage set-up

Twelve anodized aluminum frames (50 x 50 x 50 cm) were deployed in the reef with at least 1.5 m distance to each other. Three different treatments were applied to the frames (each with n = 4 replicates): (1) open cage/control (only the frame structure); (2) closed cage (frame structure surrounded with plastic net with a mesh size of 2 cm to exclude larger fishes and invertebrate grazers like sea urchins); (3) semi-closed cage (frame with closed sides but open top to only exclude large invertebrate grazers like sea urchins, but not fishes). Previous experiments have shown that exclusion nets do not cause significant caging artifacts (Miller et al. 1999, Smith et al. 2001). Each frame was equipped with 24 terracotta tiles, each with an average surface area of 168.8 ± 0.8 cm^2. Rough terracotta tiles were used, as their heterogeneous surface simulates coral rock and enhances species richness and biomass compared to other artificial substrates (Brock 1979, Fitzhardinge & Bailey-Brock 1989). Tiles were arranged pairwise on top of each other with plastic bolts and nuts, resulting in 12 upper (light-exposed) and 12 lower (shaded) tiles. Lost surface area due to drill holes and nuts was considered in calculations. To reduce sedimentation, tiles were installed in a 45 degree angle relative to the substrate on a tough plastic net fixed between the vertical poles. Every two weeks, a random pair of tiles (light-exposed and shaded)

was collected from each cage by SCUBA diving. Removed tiles were replaced by a new pair of tiles that then only stayed in the reef for the following two weeks. This procedure resulted in two data sets: (1) Long-term succession, where the development of organisms on tiles could be observed over the total study period of 24 weeks in a biweekly resolution; (2) Short-term succession, where the development of organisms within two weeks could be observed with changing start dates over the whole study period.

5.2.5 Response variables on settlement tiles

After removing the tiles from the frames, they were immediately photographed under water for following composition analyses. Afterwards, they were put in separate Ziploc bags for transportation to the laboratory. Later, all the tiles were rinsed with freshwater to remove mobile invertebrates, sediments and salt. All sessile organisms (including algae, invertebrates etc.) were scraped off with razor blades and collected in pre-combusted, preweighted tinfoil. Tinfoil packages with content were dried at 40 °C for 24 h and kept dry until analysis. Dry mass was determined with a precision balance (G&G; accuracy 0.001 g).

Quantitative differences in succession and species composition were determined using photo documentation of tiles. Pictures were analyzed with the software Coral Point Count with Excel extension (CPCe) 4.1 (Kohler & Gill 2006) using 100 randomly overlaid points which were then assigned to the following functional groups and subgroups: (1) Non biotic cover/bare terracotta; (2) Filamentous algae: Large filamentous algae (>2 mm); Small filamentous algae (<2 mm); (3) Fleshy macroalgae: brown macroalgae; green macroalgae; red macroalgae; (4) Coral (5) Sessile invertebrates other than corals: barnacles; bryozoans; polychaetes; tunicates; (6) Cyanobacteria; (7) Crustose coralline algae (CCA); (8) Crustose algae other than CCA (9) Sponges. Thereby, proportional cover for each functional group on settlement tiles was determined.

Samples from light-exposed tiles were homogenized using mortar and pestle for Elemental analysis of total carbon (C), nitrogen (N) and organic carbon (C_{org}) contents. Ground powdered samples were weighted to 1 mg and put into 10 x 10 mm silver (C_{org}) and tin (C/N) cups. For analysis of C_{org} content, 200 µL 1N HCl was added to the sample to remove $CaCO_3$ before dried again at 40 °C for 24 h. Elemental analysis was carried out with an Eurovector Euro EA 3000 elemental analyzer with a precision of ± 0.18 % for C and ± 0.13 % for N (calculated with Apfelblatt SRM 1515 standard).

5.2.6 Statistical data analysis

Statistical analyses were performed using SigmaPlot 12.5 and IBM - SPSS Statistics software. Data were tested for Gaussian distribution with normal probability plots (Q-Q-plot) and/or Shapiro-Wilk-Test prior to analysis. Data for chl *a* and nutrient analysis were grouped into

non-upwelling (Oct. - Jan.) and upwelling (Feb. - Mar.) periods and tested for differences with a t-test. Differences in cover of functional groups as well as dry mass, organic C, N content and C_{org}/N ratio were analyzed using 2-factorial analysis of variance (ANOVA) with caging (open, semi-closed, closed) and time (12 sampling times) as fixed factors. Holm-Sidak Tests were used for post-hoc pairwise comparisons. To meet assumptions of normal distribution, data for nitrogen and organic carbon (long-term succession tiles) and dry mass (short-term succession) were log(x+1) transformed prior to analysis. Correlation of the proportional cover of filamentous algae and sessile invertebrates with nitrate concentrations was tested via linear regression analysis. Additionally, the benthic community composition on settlement tiles (proportional cover) was explored with Principal Coordinate Ordinations (PCO) and statistically tested by Permutation Multivariate Analyses of Variance (PERMANOVA) in PRIMER-e v6 with PERMANOVA+ add-on. Fixed factors for analysis were (1) Time, (2) Caging and (3) Nutrient availability. Prior to analyis, the resemblance matrix of the benthic community was calculated using Bray Curtis similarity.

5.3 Results

5.3.1 Coastal upwelling and naturally increased nutrient concentrations

Chl *a* along with NH_4^+, NO_3^-, and PO_4^{3-} water concentrations were significantly higher during upwelling compared to non-upwelling season (p = 0.003, <0.001, 0.038 and 0.017 respectively; t-test). Additionally, chl *a* levels peaked between week 8 and 10 (2-fold increase compared to the mean over time) and increased after week 16 (2.5-fold). NH_4^+, NO_3^- and PO_4^{3-} increased after week 16 (4-fold, 8-fold and 4-fold respectively; compared to mean over time) (Fig. 5.2).

5.3.2 Fish surveys

During five fish surveys, a total number of n = 3235 fish was counted, belonging to 29 different species (thereof 12 herbivores). A total fish abundance of 0.86 ± 0.24 ind. m^{-2} and a total fish biomass of 51.32 ± 13.12 g m^{-2} were observed. Herbivorous fish accounted for 40 % (0.34 ± 0.07 ind. m^{-2}) in terms of abundance and 41 % in terms of fish biomass (21.19 ± 5.55 g m^{-2}). Parrotfish (*Scaridae*) were the most abundant family in the reef (32 %), followed by Damselfish (*Pomacentridae*) (30 %), Triggerfish (*Balistidae*) (10 %) and Wrasses (*Labridae*) (10 %). Parrotfish were also considered as the main roving herbivores at the study site. The only occurring species, *Scarus ghobban*, accounted for 87 % of all herbivorous fish. Surgeonfish were sometimes observed on the reef, but hardly counted during surveys. Other herbivores such as some *Acanthuridae* (1 %), *Chaetodontidae* (7 %) or *Pomacanthidae* (4

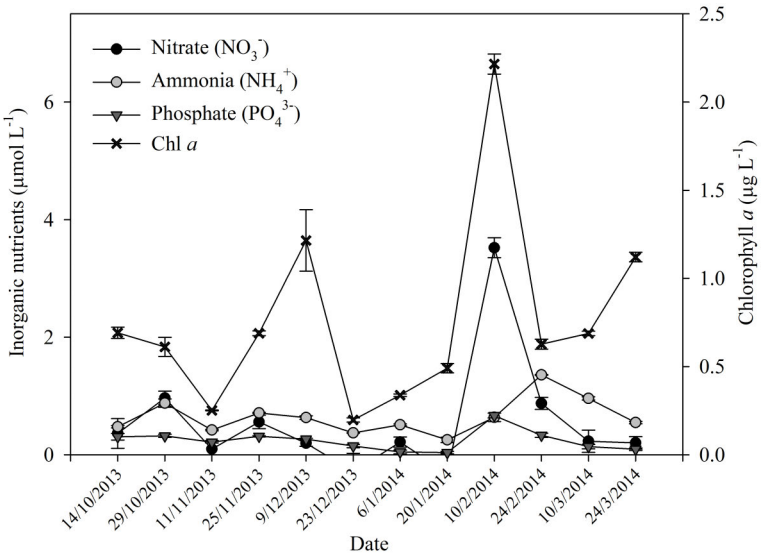

Figure 5.2: Concentrations of nitrate (NO_3^-), ammonia (NH_4^+), phosphate (PO_4^{3-}) and chlorophyll *a* in seawater. Water samples from above the reef. Values presented as means ± SE.

%) occurred in low numbers. The average fish diversity, expressed by the Shannon-Wiener Index, was 1.91 ± 0.08.

Observations on cage set-ups showed that significantly more fishes were entering open (21.0 ± 5.0 ind. fish min^{-1}) or semi-closed treatments (18.5 ± 2.5 ind. fish min^{-1}) in comparison to closed cage structures (3.0 ± 1.0 ind. fish min^{-1}) (p = 0.006, t-test). The same was observed for the number of bites per minute on settlement tiles, both on light-exposed and shaded sides. On average, light-exposed tiles in open cages experienced 9.5 ± 1.0 bites min^{-1}, whereas tiles in closed cages experienced bite rates of 1.1 ± 0.8 bites min^{-1} (p<0.001, t-test).

5.3.3 Effects of simulated overfishing

The exclusion of larger invertebrate grazers like sea urchins with semi-closed cages had no significant effect on the community composition, dry mass and organic C and N content developing on tiles compared to the controls, and thereby resembled open plots in all measured response parameters (Holm-Sidak post-hoc analysis in Table 1, 2, 3 and 4).

Simulated overfishing with closed cages resulted in significant changes in the benthic community composition: dominant functional groups on light-exposed tiles in closed cages were filamentous turf algae (50 % mean cover over time), tunicates (28 %) and fleshy macroalgae (8 %), whereas prevailing functional groups in open treatments were filamentous turf algae (60 %), bare substratum (24 %) and crustose coralline algae (9 %). No fleshy macroalgae or tunicates were observed in open cages (Fig. 5.3, Table 5.1). On shaded tiles, the

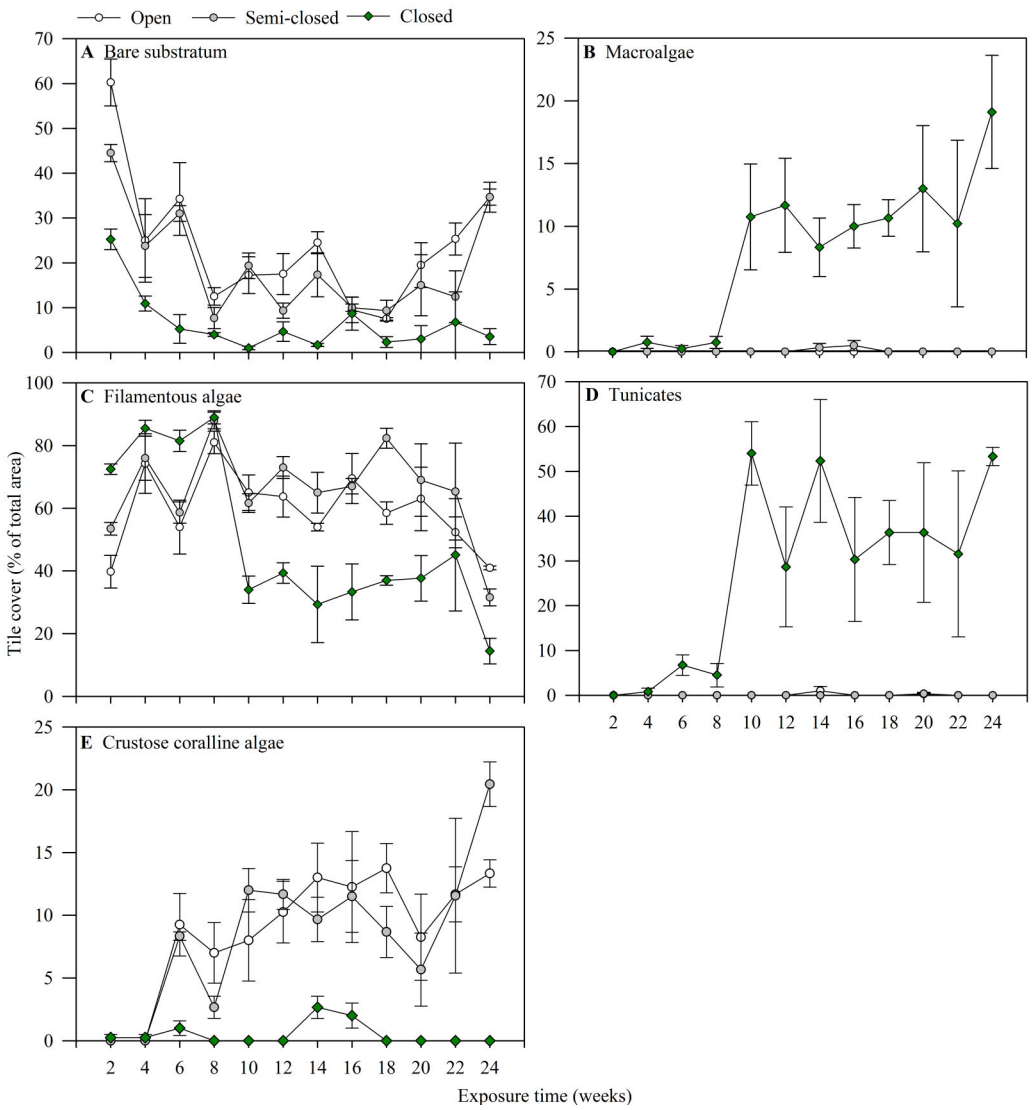

Figure 5.3: Cover of organisms on light-exposed settlement tiles (long-term experiment). Shown is the proportional cover of different functional groups (A: Bare substratum, B: Macroalgae, C: Filamentous algae, D: Tunicates and E: Crustose coralline algae) over the study period of 24 weeks in the three treatments (open, semi-closed and closed cages). Values presented as means ± SE.

exclusion of fish caused a 5-fold reduction of sessile invertebrates and a 8-fold reduction of CCA and, as on light-exposed tiles, promoted the establishment of tunicates (71 % coverage) (Fig. 5.4, Table 5.2).

Most variation in the community composition on light-exposed tiles is explained by multivariate analyses along PCO1 (66.7 %), which correlates (r = -0.74) with the factor Caging. Analysis revealed two clusters: a) caged and b) open and semi-caged settlement tiles. The community composition on caged settlement tiles was therefore significantly different from the other two treatments (Pseudo-F = 32.669, p(perm) = 0.001, perms = 997; PERMANOVA).

Further variation in the data is explained along PCO2 (25%) which correlates ($r = 0.77$) with time, indicating a succession in community composition in all treatments over the study period (Pseudo-$F = 3.934$, p(perm) = 0.001, perms = 997; PERMANOVA) (Fig. 5.5).

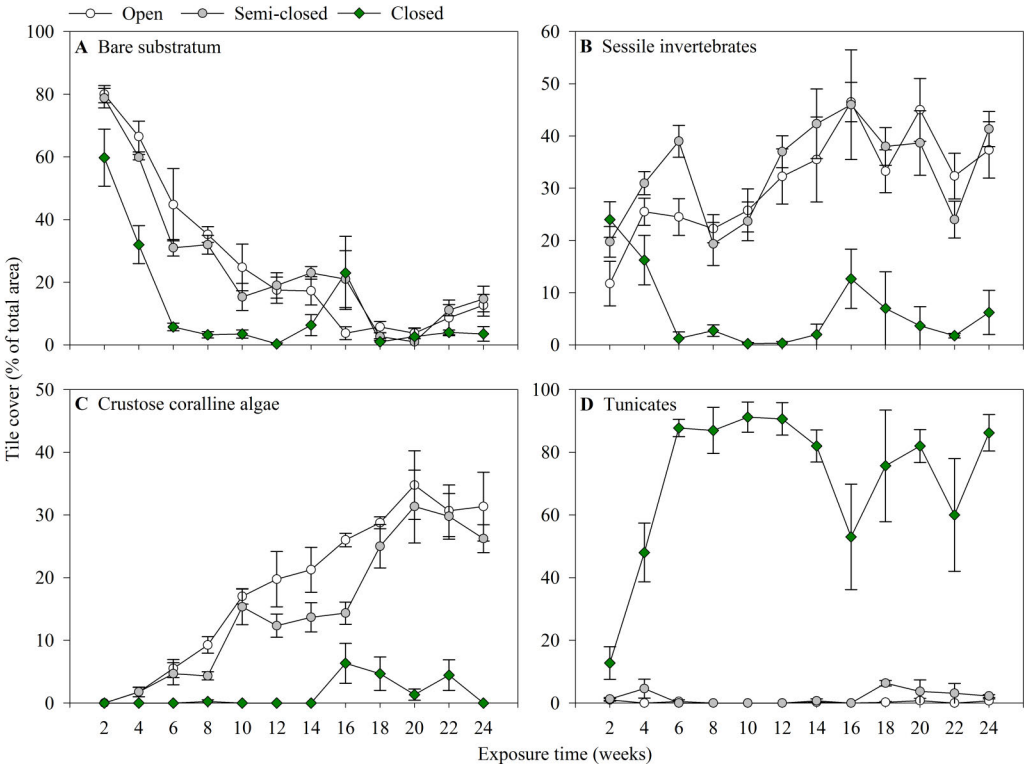

Figure 5.4: Cover of organisms on shaded settlement tiles (long-term experiment). Shown is the proportional cover of different functional groups (A: Bare substratum, B: Sessile invertebrates, C: Crustose coralline algae and D: Tunicates) over the study period of 24 weeks in the three treatments (open, semi-closed and closed cages). Values presented as mean ± SE.

Table 5.1: Results of the two-factorial ANOVA comparing effects of treatments on functional groups on light-exposed settlement tiles (long-term succession).

	Bare substratum			Macroalgae			Filamentous algae			Tunicates		
	df	F	p	df	F	p	df	F	p	df	F	p
Caging	2	26.32	<0.001*	2	20.03	<0.001*	2	6.97	0.039*	2	3.97	0.034*
Time	11	8.18	<0.001*	11	1.01	0.470	11	4.06	0.011*	11	3.06	0.012*
open vs. closed			<0.001*			<0.001*			0.031*			<0.001*
semi-closed vs. closed			<0.001*			<0.001*			0.016*			<0.001*
open vs. semi-closed			0.091			0.962			0.288			0.987

Response variables are shown in the first row, the two independent factors (Caging, Time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by asterisks.

Table 5.2: Results of the two-factorial ANOVA comparing effects of treatments on functional groups on shaded settlement tiles (long-term succession).

	Bare substratum			Invertebrates			CCA			Tunicates		
	df	F	p	df	F	p	df	F	p	df	F	p
Caging	2	10.76	<0.001*	2	38.73	<0.001*	2	24.98	<0.001*	2	201.24	<0.001*
Time	11	17.74	<0.001*	11	1.50	0.203	11	4.87	<0.001*	11	9.37	0.526
open vs. closed			0.001*			<0.001*			<0.001*			<0.001*
semi-closed vs. closed			0.002*			<0.001*			<0.001*			<0.001*
open vs. semi-closed			0.795			0.495			0.142			0.789

Response variables are shown in the first row (CCA = Crustose coralline algae), the two independent factors (Caging, Time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by asterisks.

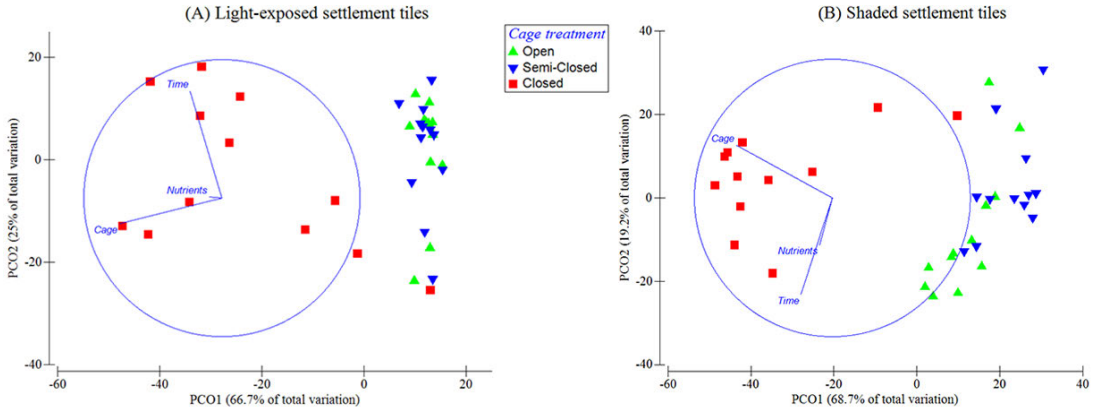

Figure 5.5: Shifts in benthic community structure on (a) light-exposed and (b) shaded settlement tiles. The distance between data points reflects their similarity in benthic community composition (close = similar) and the shift along axes can be assigned to changes in variables. On light-exposed tiles, PCO1 correlates negatively to the treatment of caging (r = -0.74) and PCO2 correlates positively to the factor time (r = 0.77). On shaded settlement tiles, PCO1 correlates negatively to the treatment of caging (r = -0.69) and PCO2 correlates negatively to the factor time (r = -0.70).

Simulated overfishing furthermore resulted in a significant increase in dry mass (11-fold), and organic C (8-fold) and N (16-fold) contents on caged tiles compared to controls, and decreased the organic C/N ratio by 30 % (Fig. 5.6, Table 5.3).

In the short-term succession experiments, simulated overfishing did not have a significant influence on the benthic community composition (Fig. 5.7) or development of organic C and N within two-week periods (Fig. 5.9, Table 5.4).

5.3.4 Effects of naturally increased nutrient concentrations caused by upwelling

Established communities on long-term succession tiles did not experience pronounced changes in composition during the study period related to naturally increased nutrient water concentrations caused by coastal upwelling. Bare terracotta tiles of the short-term succession experiments however showed a two-fold increase of filamentous turf algae in response to enhanced nutrient availability in weeks 16-18 (Fig 5.7), and turf algae cover correlated with nitrate concentrations (r^2 = 0.83; p <0.001; Fig. 5.8a). A peak of sessile invertebrate settlement could be observed with a two week delay in week 18-20 (Fig. 5.7), and invertebrate cover also correlated with nitrate concentrations (r^2 = 0.81; p <0.001; Fig. 5.8b). Dry mass along with organic carbon and nitrogen values on light exposed tiles doubled in weeks 16-18 and stayed high until the end of the experiment in March. The C_{org}/N ratio significantly decreased in all treatments (p <0.001, two-factorial ANOVA) during that period. Whereas the ratio returned to former values in open treatments within 4 weeks, it stayed low in closed cages until the end of the experiments (Fig. 5.9).

Table 5.3: Results of the two-factorial ANOVA of response parameters on light exposed tiles (long-term succession).

	Dry mass			Nitrogen			Organic carbon			C_{org}/N ratio		
	df	F	p	df	F	p	df	F	p	df	F	p
Caging	2	24.51	<0.001*	2	16.39	<0.001*	2	24.36	<0.001*	2	46.40	<0.001*
Time	10	2.71	0.022*	10	2.24	0.049*	10	147.63	<0.001*	10	7.16	<0.001*
open vs. closed			<0.001*			<0.001*			<0.001*			<0.001*
semi-closed vs. closed			<0.001*			<0.001*			<0.001*			<0.001*
open vs. semi-closed			0.777			0.882			0.741			0.054

Response variables are shown in the first row, the two independent factors (Caging, Time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by the asterisks.

Table 5.4: Results of the two-factorial ANOVA of response parameters on light exposed tiles (short-term succession).

	Dry mass			Nitrogen			Organic carbon			C_{org} / N ratio		
	df	F	p	df	F	p	df	F	p	df	F	p
Caging	2	8.29	0.002*	2	9.76	0.538	2	2.55	0.103	2	4.47	0.025*
Time	10	8.99	<0.001*	10	31.94	<0.001*	10	19.30	<0.001*	10	7.16	0.001*
open vs. closed			0.002*									0.024*
semi-closed vs. closed			0.022*									0.120
open vs. semi-closed			0.261									0.351

Response variables are shown in the first row, the two independent factors (Caging, Time) in the first column. The lower part of the table shows the results of the Holm-Sidak test for pairwise comparison. Significant differences are indicated by the asterisks.

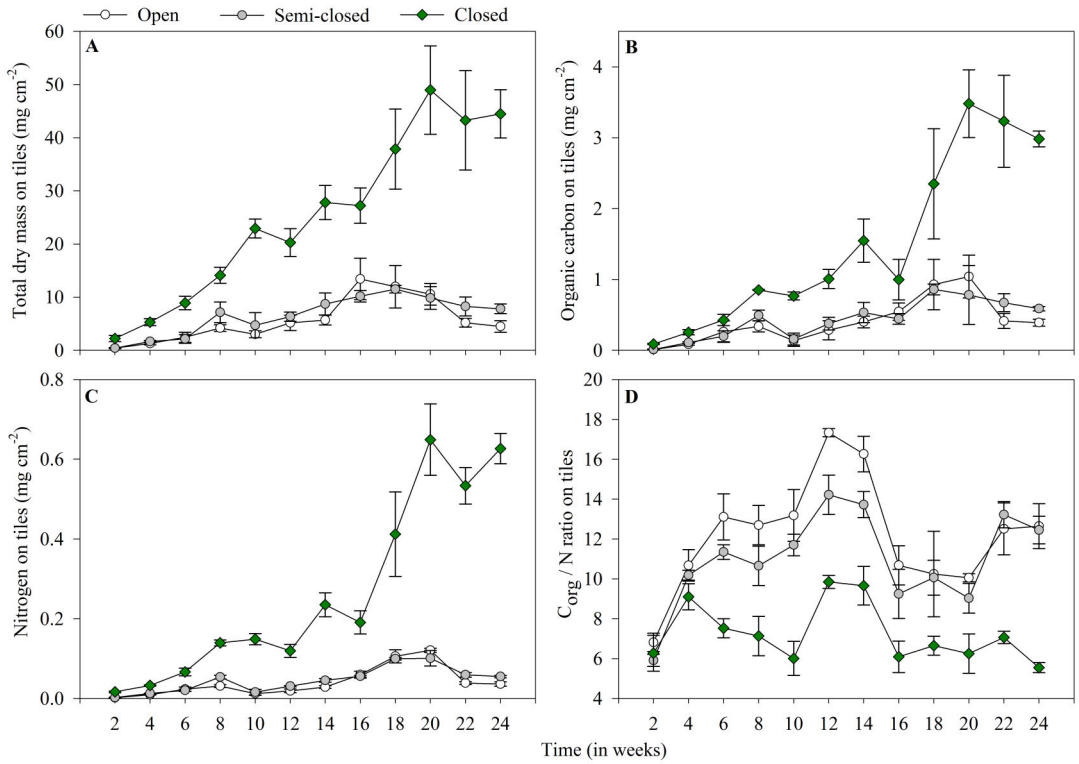

Figure 5.6: Development of total dry mass (A), organic carbon content (B), nitrogen content (C) and organic C/N ratio (D) on light exposed settlement tiles (long-term experiments). Values given as means ± SE over the study period of 24 weeks.

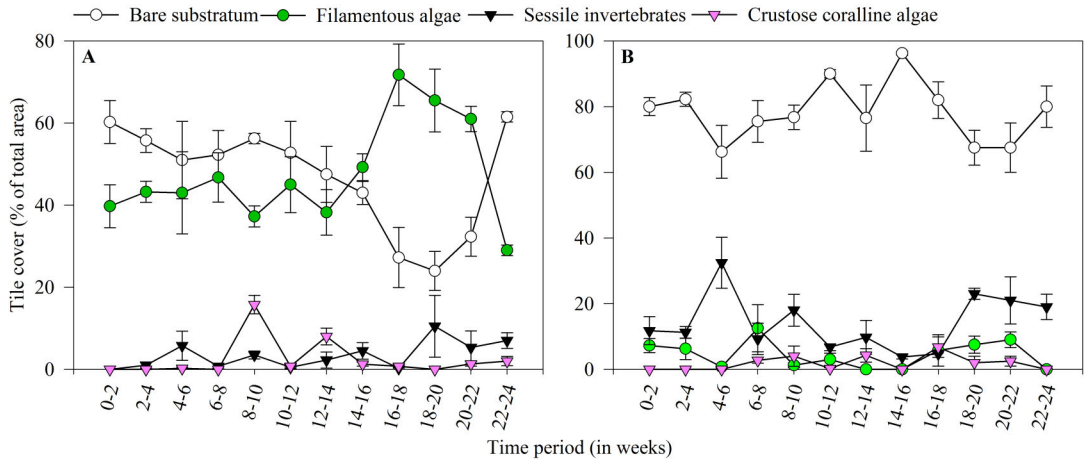

Figure 5.7: Cover of organisms on light-exposed (A) and shaded (B) settlement tiles in open cages (short-term experiment). Shown is the proportional cover of functional groups developing in the two-week periods over the whole study time. Values presented as mean ± SE. Graphs show data of open cages only, because no significant differences could be found to closed and semi-closed treatments (2-factorial ANOVA and Holm-Sidak post-hoc test).

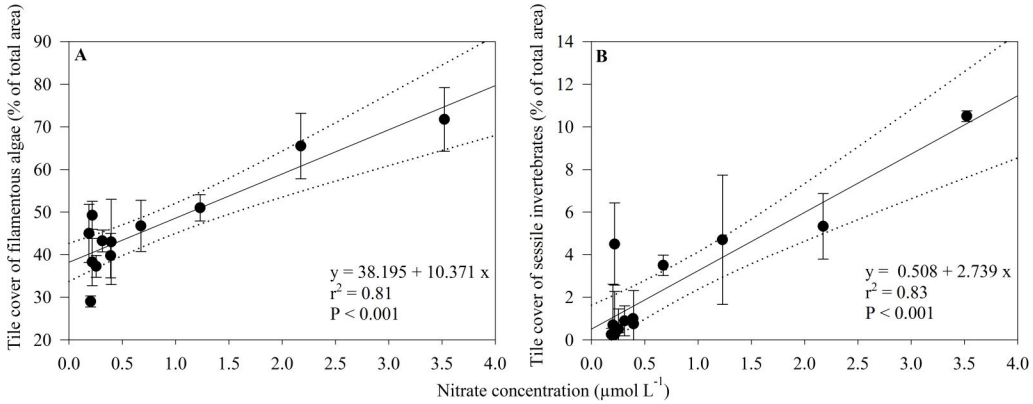

Figure 5.8: Proportional cover of filamentous algae (A) and proportional cover of sessile invertebrates (B) on light-exposed tiles in correlation to nitrate concentration. Regression analysis using nitrate concentration as independent variable. Proportional cover of sessile invertebrates is plotted with a two-week delay. Solid lines represent the regression line. Dotted lines indicate the confidence interval (95%). Normality Test (Shapiro-Wilk) and Constant Variance Test passed in both cases.

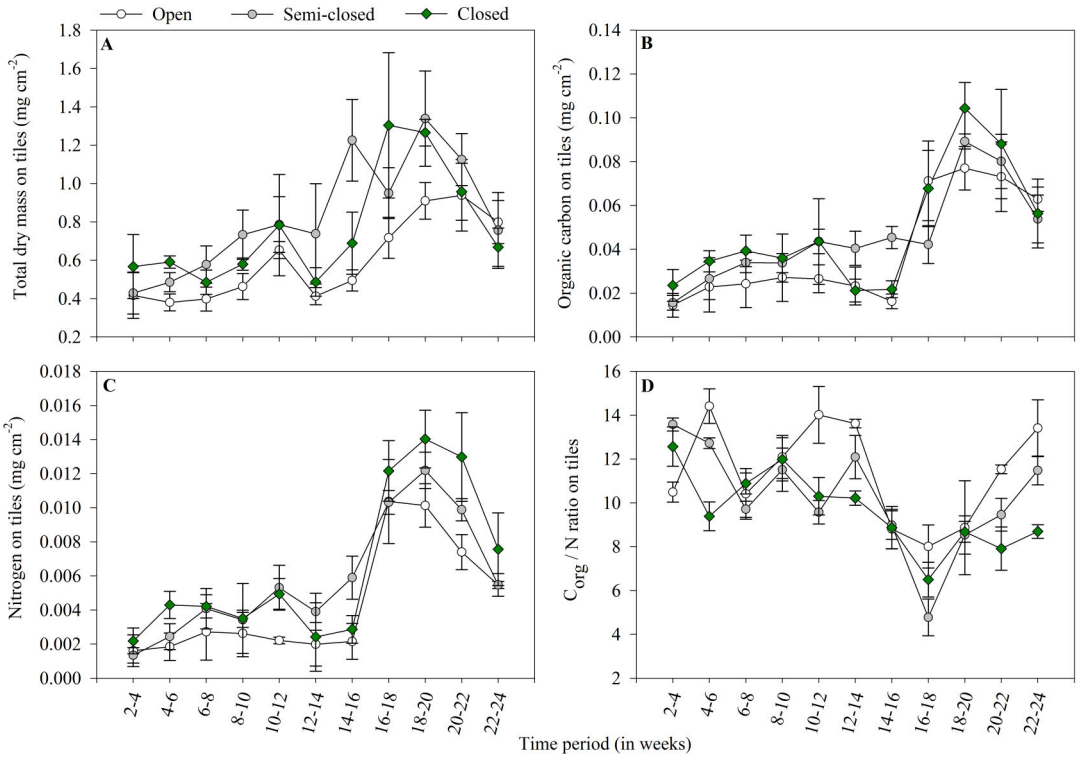

Figure 5.9: Total dry mass (A), organic carbon content (B), nitrogen content (C) and organic C/N ratio (D) on light exposed settlement tiles (short-term experiments). Values are given as means ± SE for each two-week time period.

5.4 Discussion

Concordant to several other studies (McClanahan et al. 2003, Burkepile and Hay 2009; Rasher et al. 2012; Jessen et al. 2013, Stuhldreier et al. 2015), herbivorous fish seemed to exert major control over the benthic community structure of the investigated reef. Additionally, we could show the importance of invertebrate feeding fish, as they control bioeroding and highly competitive organisms such as ascidians or sponges. Furthermore, the current study also highlights that nutrients may influence the early development of a benthic community, if present in high concentrations. In this case, upwelling derived nutrients enhanced filamentous algae growth.

5.4.1 Reef parameters

The nutrient analysis confirmed that the studied reef was seasonally exposed to coastal upwelling during the study period. Concentrations of ammonia and nitrate at the study site significantly increased during upwelling season between February and April compared to non-upwelling season. This corresponds with findings of climatological studies of Wyrtiki (1964) and Fiedler (2002), who analyzed the structure and seasonal evolution of the Costa Rica upwelling dome. Along with inorganic nutrient concentrations, the chlorophyll *a* concentration doubled within the given time frame, indicating high phytoplankton activity. Since bioavailable nitrogen is the limiting nutrient in most tropical waters where iron is available in sufficient amounts (Barber & Chavez 1991), these findings corroborate that natural eutrophication took place between February and April. Results also indicate that upwelling in the northern part of Pacific Costa Rica is not a constant event, but compromises several upwelling peaks with non-upwelling conditions in between; as previously described for Bahía Culebra (Jiménez 2001, Alfaro & Cortés 2012). This phenomenon is typical for upwelling systems around the world (Small & Menzies 1981) and related to altering wind jets (Huntsman & Barber 1977). It highlights that local benthic communities have to be highly adapted to the pronounced seasonal changes in water parameters.

A meta study of Mesoamerican Reefs showed a lower average herbivorous biomass of 14.5 g m^{-2} (Wilkinson et al. 2008) compared to our findings (21.2 g m^{-2}), indicating that Matapalo Reef corresponds to relatively unfished reefs in Central America. However, the comparison of such data is questionable since regional differences in species composition and richness due to their evolutionary history and oceanographic condition might exist. No comparable data on herbivorous biomass of Pacific Costa Rica is published.

5.4.2 Effects of simulated overfishing

Sea urchins (e.g. *Diadema mexicanum*) and other large invertebrate herbivores were never observed in experimental plots, although they were abundant in the surrounding reef (5.31 ± 0.36 ind. m^{-2}; Stuhldreier, unpublished data). Likewise to experiments by Jessen et al. (2013) with similar cage constructions, the experimental cage set-up seemed to disable sea urchins to reach the settlement tiles deployed within cage structures. Their influence on the experimental results is therefore negligible, even though sea urchins may play a major consumer role as herbivores in coral ecosystems (Roff & Mumby 2012). Herbivorous fish were efficient in the removal of fleshy brown macroalgae of the genus *Dictyota* sp., which were only present in closed cages. This result is concordant with other studies, where fleshy brown algae were found on experimental tiles after a few weeks (Burkepile & Hay 2009, Smith et al. 2010). Frondose macroalgae are particularly attractive to herbivores (Hay 1984, Littler & Littler 1984) and become abundant only when grazing pressure is reduced, suggesting that they can serve as indicators for overfishing in coral reefs (Cooper et al. 2009). Similar to studies by Burkepile & Hay (2009), Smith et al. (2010) and Chadwick & Morrow (2011), the exclusion of fish in the present study reduced the recruitment of sessile invertebrates such as barnacles and polychaetes and inhibited the settlement of crustose coralline algae. Instead, the colonial ascidian *Didemnum* sp. rapidly dominated cover on shaded and light-exposed tiles in caged treatments. Even though ascidians typically constitute a small component of the benthic community on coral reefs (Chadwick & Morrow 2011), studies have shown a strong potential of dispersal, spreading and even overgrowth if predators are lacking or nutrients are increased (Lambert 2002, Shenkar et al. 2008, Stuhldreier et al. 2015). The low dispersal range of *Didemnum* sp. with only 10 m distance (Bak et al. 1996) suggests that colonies must have been already present in the studied reef. Benthic surveys in the immediate vicinity of the experimental plots did not show any colonies of *Didemnum* sp. (Sánchez, unpublished data). Thereof, one has to consider that the artificial substrate might facilitate *Didemnum* sp. settlement. However, by scanning the reef with a close look between branching corals, the ascidian was found at the base of many *Pocillopora* colonies. This implies that *Didemnum* sp. is able to grow where predator fish have limited access, regardless of the substratum. The successful establishment of *Didemnum* sp. in Eastern Pacific coastal waters of Central America is a newly observed phenomenon and outbreaks on the west coast of North America have only been reported within the last decade (e.g. Lambert & Lambert 2003, Bullard et al. 2007). Ascidians closely related with the genus *Didemnum* have simultaneously undergone rapid population expansions worldwide. Bak et al. (1996) reported a 9-fold increase in the density of *Trididemnum solidum* over a period of 15 years in a Caribbean reef and Witman & Smith (2003) showed a 3-fold increase of ascidian biomass in a reef of Galapagos within one year, underlining the strong competitive

potential of colonial ascidians which may further benefit from anthropogenic stressors (e.g. invasion of species, reduced predation pressure and high nutrient concentrations).

Dry mass along with organic carbon and nitrogen contents on settlement tiles showed a significant increase when fishes were excluded from experimental plots. This confirms previous experiments (McCook et al. 2001, Smith et al. 2001, Hughes et al. 2007, Smith et al. 2010, Jessen et al. 2013, Tamai & Sakai 2013), suggesting the efficient reduction of algae-derived organic matter by herbivorous fish. Results of the present study support the findings of Jessen et al. (2013), where herbivores efficiently removed algal N content on settlement tiles (27-fold decrease compared to controls). The lower C_{org}/N ratio in closed cages compared to controls implies that herbivores particularly fed on nitrogen rich algae in open treatments, likely to maximize their foraging efficiency (Mattson Jr 1980, Minkenberg & Ottenheim 1990, Goecker et al. 2005).

5.4.3 Effects of naturally increased nutrient concentrations caused by upwelling

Coastal upwelling between February and April did not result in visible effects on the established benthic community on long-term succession tiles, however significantly increased the relative proportional cover of filamentous algae on the two-week succession tiles. In this case, filamentous algae were able to outcompete other algal groups and organisms by their fast colonization of light-exposed substratum (Borowitzka et al. 1978, Kendrick 1991). This demonstrates that nutrient enrichment can influence coral reef community composition without requiring experimentally reduced herbivory, which is concordant to a recent study by Muthukrishnan & Fong 2014. The decreased C_{org}/N ratio during weeks 16-18 on light-exposed tiles indicates an effective uptake of available nutrients resulting in algal growth (Atkinson & Smith 1983). Similar results have been reported before (Smith et al. 2001, Lapointe et al., 2004; Littler et al., 2006, Vermeij et al. 2010), where a significant increase of filamentous turf algae in response to elevated nutrient concentrations was shown. As primary producers, filamentous algae are likely to take advantage from high nutrient conditions (Carpenter 1990) and may therefore represent a good indicator for high ambient nutrient concentrations. Linear regression analysis also indicated that barnacles indirectly benefited from elevated nutrient levels in seawater. Nutrients provided by coastal upwelling can lead to an increase of phytoplankton biomass and the production of particulate organic carbon (Small & Menzies 1981). Filter-feeding organisms can therefore benefit from higher food availability (Hallock 2001), which makes them strong competitors for space under more eutrophic conditions (Birkeland 1977). The increased occurrence of barnacles followed increased nutrient concentrations with a delay of two weeks. This period may represent the time the trophic cascade needs to transform nutrients to available food particles for filter-feeding organisms (Croll et al. 2005).

5.5 Concluding remarks

Concordant to studies from all over the world, these results support the importance of a healthy and abundant fish community in coral reefs (e.g. Burkepile & Hay 2006, Hughes et al. 2007, Rasher et al. 2012, Muthukrishnan & Fong 2014, Stuhldreier et al. 2015). The lac of herbivorous fish can lead to pronounced changes in the benthic community with shifts to algal dominated states. This accompanies with a reduced coral recruitment and survivorship, strong sedimentation and unconsolidated substratum. Herbivores thus play a crucial role in coral reef resilience by limiting the development and growth of algal communities that impede coral establishment. However, our study from the Eastern Tropical Pacific has shown an additional successful and strong competitor for space if predatory fish are missing. The colonial ascidian *Didemnum* sp. has the potential to cause great ecological and economic damage due to its rapid proliferation and strong competitive abilities when predation pressure is lowered. Considering that large coastal areas of Pacific Costa Rica are already impacted by the overexploitation of fish (Wehrtmann & Nielsen-Muñoz 2009), remaining coral reefs, such as Matapalo, are threatened if not protected and managed appropriately. The ability of fleshy macroalgae and the colonial ascidian *Didemnum* sp. to dominate reefs should therefore be considered and their presence used as indicators of overfishing. Supplementary, coral reefs in the studied area are influenced by seasonally elevated nutrient concentrations due to coastal upwelling. While there is no direct impact visible on an established benthic community, bare substratum (e.g. after disturbances such as storms) is dominantly colonized by fast growing turf algae, intensifying the problems related to overfishing. This indicates that nutrient enrichment can influence coral reef community development and composition even without requiring experimentally reduced herbivory. Integrated management strategies to improve coral reef health in the northern part of Costa Rica should therefore prioritize on such local key drivers of resilience and further monitor the coral reef health status under the above stated aspects.

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6 Massive coral tissue ablations in reefs of Pacific Costa Rica

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In January 2012, we observed massive tissue ablations of many scleractinian coral colonies of the genus *Pocillopora* (*P. elegans* and *P. damicornis*) in between 3 and 7 m water depth at location Matapalo Reef (10.538391 N, 85.765930 W) at the Northern Pacific coast of Costa Rica (Fig. 6.1). This was the most drastic direct coral dying event the authors have ever observed in more than 1,500 dives in coral reefs around the world during the last decade. More than 50 % of all observed Pocillopora coral colonies (n = 48) were affected, and no coral bleaching as intermediate response was visible. There were few other hard coral colonies of the genera *Psammocora*, and *Pavona* present, but none of these massive corals exhibited the tissue ablations that were observed for *Pocillopora*. Reason for this event was not evident, because none of simultaneous measurements of water quality (pH = 8.2, water temperature = 27 °C, salinity = 33, O_2 concentrations close to saturation) showed atypical values.

Despite the detachment of tissue fragments from coral skeleton has been noted in the field and in the laboratory in response to environmental stress (Sammarco 1982, Richmond 1985), and although soft tissue detachment from the skeleton of colonial scleractinian corals has been observed both in vivo and in vitro (Domart-Coulon et al. 2005), such massive coral tissue detachment and ablation at the scale observed here has never been reported for Eastern Tropical Pacific reefs in the literature before. However, this phenomenon may potentially be related to infection by pathogenic bacteria of the genus *Vibrio* as described by Ben-Haim et al. (2003) and Luna et al. (2007).

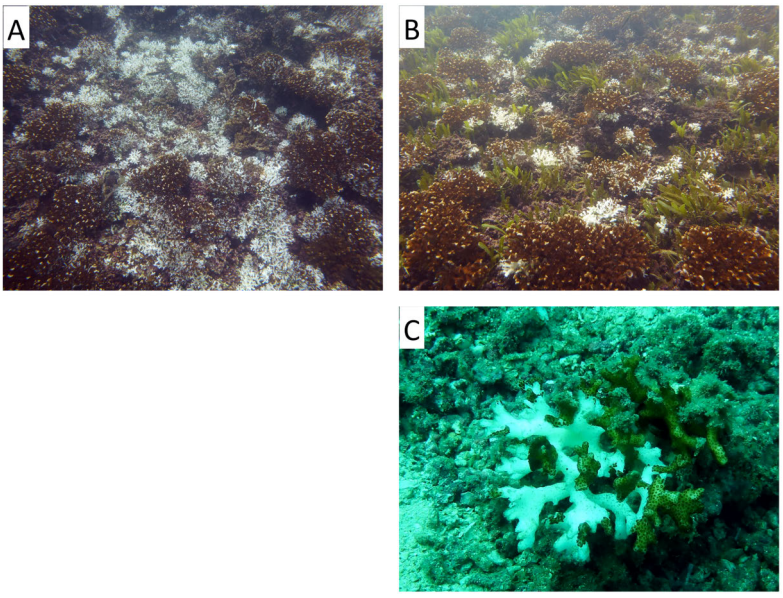

Figure 6.1: Tissue ablations of coral colonies of the genus *Pocillopora* (*P. elegans* and *P. damicornis*) at Matapalo Reef, Costa Rica (A and B) and close-up of tissue ablations of a single *Pocillopora* cf. *damicornis* coral colony (C)

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7 General discussion

7.1 Key findings and significance

The large-scale degradation of coral reef ecosystems worldwide may result in the decline of ecosystem productivity and functioning with consequent loss of associated ecosystem services (Hoegh-Guldberg et al. 2007). The impact of local and global stressors on coral reef assemblages will depend on the magnitude of exposure, and the ability of individuals to acclimatize (physiological adjustments) or populations to adapt (genetic modification over generations) to the variability in their environments (Palumbi et al. 2014). Acclimatization and adaptation potential is a hot topic in coral reef research, but in situ studies investigating ecosystem responses are scarce.

This thesis provides a valuable contribution to the understanding of coral reef functioning in naturally variable environments. The upwelling influenced Gulf of Papagayo provided an ideal natural laboratory for this research, hosting structurally simple coral reef communities that experience predictable changes in environmental parameters. For the first time in an upwelling system, this study simultaneously evaluated a range of abiotic and biotic status- as well as process-variables on a coral reef over an entire observation year. The high temporal resolution of samplings and observations was unique in coral reef research, and the extensive data set enabled direct correlations between environmental parameters and ecosystem composition and production. This thesis represents the most comprehensive study of coral reefs in the Gulf of Papagayo, and the five chapters combined provide a holistic view of the factors driving local coral reef functioning (Fig. 7.1).

7.1.1 Effects of upwelling on water column parameters

The physicochemical environment of the studied reefs changed substantially during a major upwelling period from February to April 2014 (Chapter 2). These changes in water parameters were more pronounced at the northern site, confirming the proposed gradient in upwelling intensity. The effect on temperature was inferior compared to other tropical upwelling areas (Schmidt et al. 2012, Bayraktarov et al. 2014) and maximum nitrate concentrations were lower than concentrations measured in other eastern Pacific upwelling

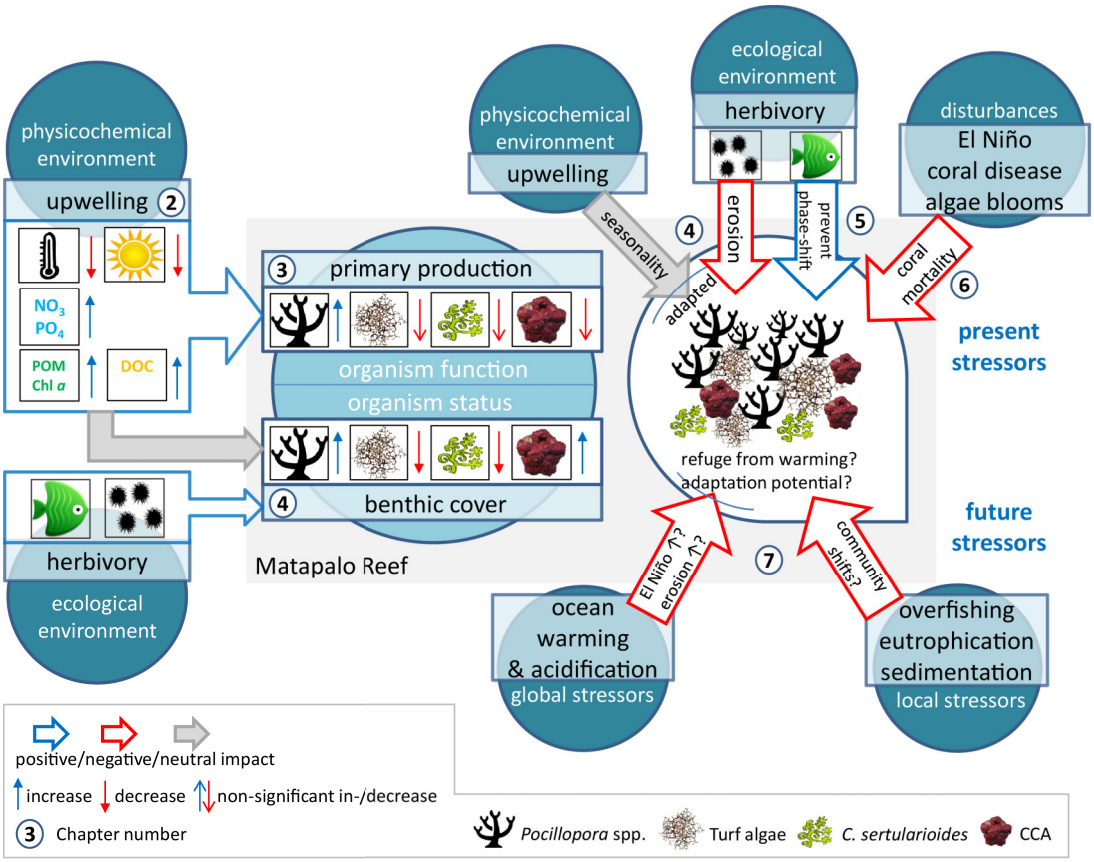

Figure 7.1: Graphical synopsis of thesis results. The studied reef Matapalo is represented by the grey box, addressing responses on organism (left), and ecosystem level (right). Investigated key organisms were the hard corals *Pocillopora* spp., turf algae, the green macroalga *Caulerpa sertularioides* and crustose coralline algae (CCA). The seasonal Papagayo upwelling caused pronounced changes in the physicochemical environment of the investigated reefs (Chapter 2). These changes in water parameters differently affected the photosynthetic rates of reef primary producers (Chapter 3). Changes in the benthic community however were not influenced by the seasonality in water conditions, but revealed a shift from turf algae to coral dominance which was supported by high herbivorous pressure (Chapter 4). The benthic reef community was well adapted to seasonal changes in conditions, but is threatened by sea urchin erosion (Chapter 4) and acute disturbances such as coral diseases (Chapter 6). To increase the resilience of local reefs, it is essential to retain a healthy fish community that controls algae and invertebrate communities in the investigated reef (Chapter 5). Additional global and local stressors may negatively impact local coral reefs in the future, but may be mitigated by the high adaptation potential of reef organisms to changing conditions (Chapter 7).

regions (Zuta & Guillén 1970, D'Croz & O'Dea 2007). However, sequential impacts on organic water column parameters such as chlorophyll *a* and organic matter concentrations were more pronounced and long-lasting than ever reported elsewhere. This indicates a very effective conversion of upwelling inorganic nutrients into organic matter at the study site. The results add important understanding of upwelling influences on coral reefs as they indicate that influences go beyond the effects of temperature or nutrient concentrations ad-

dressed in previous studies. Remote sensing approaches (Brenes et al. 2003) and sampling of the open water column in the Gulf of Papagayo (Rixen et al. 2012) were not able to detect the cascading effects of upwelling on organic parameters in reef waters, emphasizing the importance of in situ monitoring studies. From the results of Chapter 2, upwelling can be considered the key driver that controls productivity and nutrient recycling in coral reefs at the northern Pacific coast of Costa Rica. This may have serious implications for benthic community composition and ecosystem services (investigated in Chapters 3 - 5).

7.1.2 Effects on benthic community composition and ecosystem services

Surprisingly, our findings characterized the investigated reef as a highly dynamic benthic community that was hardly influenced by the pronounced seasonality in environmental conditions during the study period. The reef organisms were not only able to tolerate low temperatures, but even buffered upwelling-induced changes in oxygen and pH, which were detectable in the open water column (Rixen et al. 2012), but not in the reef waters (Chapter 2). Physiological processes are expected to react fastest to changes in environmental conditions. Accordingly, net primary production rates of dominant reef organisms were influenced by changes in key water parameters (Chapter 3). However, the effects of upwelling were smaller than expected, because opposing changes in different water parameters mitigated each other's effects on the organisms' physiology. Interestingly, the corals *Pocillopora* spp. were the only primary producers in the reef that benefitted from upwelling conditions, while production rates of all investigated algal taxa decreased in response to low water temperatures and light availability. These results stand in contrast to studies in other upwelling regions which found largely increased production rates for algae during upwelling (Eidens et al. 2012, 2014, Jantzen et al. 2013) and suggests a high acclimatization and competitive potential of local corals.

The benthic community composition did not follow the seasonal cycle in environmental conditions, but shifted from turf algae to hard coral dominance over the year (Chapter 4). The observed annual increase rate in coral cover of almost 30 % is among the fastest reported in the scientific literature (Diaz-Pulido et al. 2009, Graham et al. 2011). The trajectory of the reef towards coral dominance was supported by high abundances of herbivores. During upwelling, cover and biomass of turf algae on settlement tiles almost doubled in response to increased nutrient concentrations, independent of feeding pressure by herbivorous fish (Chapter 5). However, relative turf algal cover in the established reef community did not increase during upwelling season (Chapter 4), suggesting that effects of upwelling on single organisms were buffered within the reef community. High abundances of sea urchins likely limited turf algal growth in the reef, and thereby supported crustose coralline algae (CCA) and coral cover increase. Sea urchins of the genus *Diadema* not only support

very high grazing rates, but may also increase the productivity of turf algal communities by reducing self-shading, and by fertilizing the algae via ammonia excretion (Carpenter 1986). Supportively, individual net production rates of turf algae in the reef were high compared to other studies (Chapter 3). The importance of sea urchins for reef ecosystem state has been shown for the Caribbean (Lessios 1988, Knowlton 1992, Hughes 1994) but was not recognized for the eastern tropical Pacific until now. An ubiquitous indicator of ecosystem health is the presence of herbivorous fish. The experimental exclusion of fish resulted in pronounced community changes on settlement tiles from short turf algae and CCA to long turf algae, macroalgae and ascidian dominance (Chapter 5). This is in concordance with previous manipulation experiments (Belliveau & Paul 2002, McClanahan et al. 2003, Burkepile & Hay 2006, 2009, Rasher et al. 2012, Jessen et al. 2013) and emphasizes the importance of herbivorous and invertebrate feeding fish in controlling local benthic coral reef communities.

In contrast to turf algae and CCA, which were apparently top-down controlled, the cover and reproductive cycle of the macroalga *Caulerpa sertularioides* may primarily be nutrient controlled. Growth and biomass of *C. sertularioides* and *Sargassum liebmannii* in the Gulf of Papagayo increased largely in response to elevated nutrient concentrations during upwelling in previous years (Fernández-García et al. 2012, Cortés et al. 2014), which shows that the upwelling has the potential to cause significant alterations in benthic community composition. Contrary to these previous findings, no increase in macroalgae was observed in the upwelling season 2013/2014. As years differ in upwelling intensity (Alfaro & Cortés 2012), inter-annual variability in conditions and community response is likely to occur, which is supported by findings in a Caribbean upwelling system (Eidens et al. 2014). Especially with regard to regular El Niño influences on local reefs, it is therefore recommended to establish a long term monitoring of key environmental factors and reef communities in the Gulf of Papagayo to further advance the understanding of temporal dynamics in local coral reefs.

In contrast to previous studies, monitoring in a weekly resolution enabled us to observe fine-scale dynamics in benthic community composition and production which provides a valuable baseline for future studies. Together, the studies of this thesis showed that coral reef organisms differ in their responses to upwelling conditions, and that upwelling-impacted water parameters are able to mitigate each other in their effects on reef organisms. While macroalgal cover may primarily be controlled by seasonal nutrient input, herbivory was the most important factor in determining overall reef community composition.

7.1.3 Ecological perspective of local reefs

Present The studies in the present thesis illustrate that the investigated coral reef community is physiologically acclimatized to seasonally changing environmental conditions. Brown (1997) concludes in her review that coral populations subject to wide temperature ranges are likely also genetically accommodated to local conditions and therefore less sensitive to temperature variations. However, although coral reefs in the Gulf of Papagayo are resistant to upwelling, they are very sensitive to acute disturbance events. Occurrences of mass coral mortality have been reported along the coast of Costa Rica and were attributed to coral disease (Chapter 6), siltation (Jiménez 2001), harmful algal blooms (Guzmán et al. 1990) and El Niño warming events (Glynn 1990, Guzmán & Cortés 2001, Jiménez et al. 2001). Coral tissue necrosis (as reported in Chapter 6) also affected colonies of *Pocillopora* spp. during the present study, but in contrast to 2012 did not spread considerably over the reef (I. Stuhldreier, unpublished data). Harmful algae blooms and one event of fish mortality occurred in the area during the study period (personal observations), but their causes remain uncertain. Our observations emphasize the importance of identifying the agents and progression of these disturbances to improve local coral reef management.

For the first time since 2007, this thesis reported increasing coral cover at the study site, which is an optimistic sign for reef recovery from past disturbances. However, the reef did not increase in biodiversity and stability, and therefore remains vulnerable to chronic environmental and anthropogenic stressors. We found that simulated overfishing resulted in pronounced changes in algae as well as invertebrate communities (Chapter 5), emphasizing the sensitivity of local ecosystems to overexploitation of herbivorous and invertebrate feeding fish. The presence of long filamentous turf algae and ascidians are suggested as a valuable local bioindicator for overfishing, complementing the list of potential indicators of anthropogenic stressors proposed by Cooper et al. (2009). Importantly, besides herbivorous fish, sea urchins controlled turf algae abundance at the study site (Chapter 4). On the negative side, excessively high abundances of urchins largely reduce the stability of local reefs by bioerosion (Alvarado et al. 2012). Together with poor cementation of eastern tropical Pacific corals (Manzello et al. 2008), this may threaten the reefs in the Gulf of Papagayo despite high individual coral growth rates (Jiménez & Cortés 2003) and fast coral cover increase (Chapter 4). Bioerosion has already exceeded carbonate deposition in other reefs of the eastern tropical Pacific (Glynn 1988, Eakin 1996, Reaka-Kudla et al. 1996, Alvarado et al. 2012), and is therefore a realistic threat to the studied reefs.

Future On a larger temporal scale, the investigated ecosystem will be increasingly impacted by global and local stressors which lead to coral reef degradation worldwide (Hoegh-Guldberg et al. 2007, Burke et al. 2011). Therefore, the question arises how reefs in this al-

ready challenging environment will perform under future climate change scenarios. Reefs in the upwelling regions of the eastern tropical Pacific are already characterized by poor reef development and cementation due to low aragonite saturation states (Manzello et al. 2008). The threat of erosion rates overtaking carbonate accretion on local reefs could be intensified by future ocean acidification (Hoegh-Guldberg et al. 2007). The resilience of reef communities to environmental stress depends on the environment that the organisms are conditioned to, including temperature anomalies and varying nutrient and pH levels (Freeman et al. 2012). The ability of local coral reefs to withstand large seasonal fluctuations may therefore indicate their potential to adapt to future climate change. Furthermore, a recent study modelling future environmental conditions on coral reefs demonstrated that marginal reef ecosystems at high latitudes and in the eastern tropical Pacific perform well in climate change scenarios (Freeman 2015). Upwelling can reduce or delay the susceptibility of corals to bleaching via decreasing thermal and radiative stress (Glynn & D'Croz 1990, Wall et al. 2015), and may furthermore minimize post-bleaching mortality by provision of heterotrophic food resources (Grottoli et al. 2006). Upwelling regions were therefore suggested to provide refuges from future climate change (Riegl & Piller 2003, Chollett & Mumby 2013). However, the attenuation of climate change effects is only possible when warming event and upwelling coincide, and the effectiveness of upwelling in reducing thermal stress differs geographically (Chollett et al. 2010). In the Gulf of Papagayo, upwelling likely mitigated the negative effects of warming events on coral growth during the 1991-1992 (Jiménez & Cortés 2003) and the 1997-1998 (Jiménez et al. 2001) El Niños. Whether future warming events will increase bleaching in the eastern tropical Pacific is difficult to predict, as past El Niño events have largely differed in their impacts, and bleaching susceptibility is dependent on regional historical patterns of thermal stress (Glynn et al. 2001).

The results of these studies encourage research on the genetic population structure of local reefs, as genetic variations in coral host and symbiotic algae may largely affect bleaching severity in corals (Brown 1997, Rowan et al. 1997). Together with detailed knowledge about prevailing environmental conditions, the information about genetic diversity within the populations or ecosystems will help to assess the suitability of the Gulf of Papagayo as a refuge area for coral reefs under future climate change.

7.2 Outlook

Upwelling-influenced reefs in the eastern tropical Pacific provide an example of how reefs may look in the future. Subjected to low aragonite saturation states and fluctuating conditions, these reefs are simple in structure and biodiversity, but resistant to their highly variable environment. Similarly, chronic anthropogenic stress may select for a minority of resilient coral species to dominate future coral reefs (Darling et al. 2012, Graham et al.

2014). Despite their resilience towards prevailing chronic stressors, recovery of these reefs will be affected by the intervention of other disturbances (Brown 1997). These could be El Niño warming events or coral diseases, from which the 'simple' reefs will recover poorly due to low genetic diversity and functional redundancy in the coral populations. Low coral diversity, poor recovery of reefs and exposure to frequent perturbations are already observed in the eastern tropical Pacific (Cortés 1997), which therefore provides a valuable laboratory to study future reef ecosystem functions and services. The results of this thesis suggest that those future reefs may still support a high productivity and have a high resilience towards chronic stress, but are sensitive to the intervention of acute stressors. The fate of coral reefs along the Pacific coast of Costa Rica in particular, but also in general, will thus depend on the frequency and nature of disturbances in combination with the prevailing conditions in the reef that facilitate or impede recovery. In this regard, efforts have to be made to reduce local chronic stressors by decreasing nutrient input from land and regulating fishing pressure.

For reef management in the Gulf of Papagayo, the results of the present thesis highlight the importance of retaining a healthy herbivore community, as local benthic communities were predominantly top-down controlled. The proposed indicators of overfishing and the prevalence of the observed coral disease should be quantified in regular reef assessments as cost-effective and relatively easy measures of ecosystem state. As the upwelling may mitigate effects of El Niño events and future global warming, management and protection must be implemented in the Gulf of Papagayo to serve as a refuge and reservoir for coral species at the northern Pacific coast of Costa Rica.

The value of our findings extends beyond local reef management. Currently, effort is invested to find the 'fittest corals' for restoration projects, and to establish a 'seed bank' of coral gametes and embryos from extreme settings, where corals persist despite marginal conditions (Mascarelli 2014). Another area of current research investigates what makes some corals more resilient than others on a genetic level (Barshis et al. 2013, Palumbi et al. 2014, Bay & Palumbi 2015). Such efforts may be valuable for future reef restoration, and corals of the Papagayo upwelling system are potential candidates for such projects. But more importantly, recent recommendations for management are turning away from approaches trying to return pristine ecosystem configurations, and instead encourage research to understand novel coral reef ecosystem compositions and functions (Côté & Darling 2010, Graham et al. 2014). The results of this thesis contribute to the understanding of coral reef functioning in a challenging environment and highlight the potential of the Gulf of Papagayo to serve as test site for further research into the mechanisms and consequences of coral reef response to a variable future.

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Additional Publications

Peer-reviewed:

Ines Stuhldreier, Pepe Bastian, Eike Schönig, Christian Wild
Effects of simulated eutrophication and overfishing on algae and invertebrate settlement in a coral reef of Koh Phangan, Gulf of Thailand
The data for this manuscript were collected and analyzed for the preparation of I. Stuhldreier's and P. Bastian's Master theses. The manuscript was written by I. Stuhldreier with support of all authors. This manuscript has been published in Marine Pollution Bulletin, 92: 35-44 (2015)

Conference proceedings:

The results of this thesis have been presented in oral presentations and posters at international conferences.

- **2014** 4th international CORE Symposium, Bremen, Germany
  Talk: One-year monitoring of coral reef functioning in upwelling-influenced north western Costa Rica
- **2014** YouMaRes 5.0, Conference for Young Marine Researchers, Stralsund, Germany
  Talk: Coral reef functioning in upwelling-influenced reefs at the Pacific coast of Costa Rica
- **2014** ECC2014 Conference for Marine and Climate Research, Bremen, Germany
  Poster: Coral reef functioning in upwelling influenced north western Costa Rica
- **2014** Reef Conservation UK Conference, London, United Kingdom
  Poster: Effects of seasonal upwelling on coral reefs of Pacific Costa Rica
- **2015** Annual Meeting of the Society for Tropical Ecology, Resilience of tropical Ecosystems, Zürich, Switzerland
  Talk: Highly dynamic benthic communities in upwelling exposed Costa Rican coral reef
- **2015** 5th international CORE Symposium, Bremen, Germany
  Talk: Coral reef functioning in a highly variable environment - Effects of upwelling on Pacific coral reefs of Costa Rica

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